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# 7

## NEMATODE PESTS OF CEREALS

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### Introduction

Cereal seeds provide food rich in starch with about 10% protein and several micronutrients and, increasingly, raw material for industrial uses. The two groups of temperate cereals are: (i) small grains, wheat and barley originating from Eurasia and oat and rye, from the Mediterranean Basin and Europe; (ii) maize and sorghum from America and Africa, respectively. Selection by farmers and, more recently, by plant breeders has produced cereals for spring and winter sowing, adapted to diverse climates and agroecosystems, where cultural practices and potential yields also vary greatly. World production is summarized in Table 7.1.

Cereal nematodes have been regularly reviewed; in cool temperate regions (Kort, 1972; Caubel *et al.*, 1980; Griffin, 1984; Hirling, 1984), Mediterranean and semi-arid areas (Sikora, 1988) and in the tropics and sub-tropics (Swarup and Sosa-Moss, 1990). We have summarized recent biological and technical information on the important parasites, but have cited selected references only.

### Small Grain Cereals

Wheats comprise the widely grown soft wheat (*Triticum aestivum* var. *vulgare*) and durum wheat (*T. turgidum* var. *durum*), mainly grown in dry regions. Barley (*Hordeum vulgare*) is well adapted to less favourable cultural conditions and is grown for animal feed and malt. Oat (*Avena sativa*), rye (*Secale cereale*) and triticale, derived from rye × wheat hybridizations, are less important.

### CYST NEMATODES

Cereal cyst nematodes constitute a complex of several closely related species,

Table 7.1. Changes in world cereal production, 1954–1988<sup>a</sup>.

	Wheat <sup>b</sup>	Barley	Oats	Rye	Maize	Sorghum and millets
AREA: million ha 1954	188	64	54	35	99	111
percentage increase (1954 = 100)						
1968	121	117	59	63	107	100
1977	123	142	57	40	120	98
1986	121	125	46	44	129	78
1988	117	120	41	46	129	77
YIELD: t ha <sup>-1</sup> 1954	0.81	1.05	0.93	0.58	1.54	0.66
percentage increase (1954 = 100)						
1968	181	167	182	260	154	116
1977	206	182	185	298	192	137
1986	291	217	206	361	247	169
1988	286	206	183	350	204	168

<sup>a</sup> Source FAO year book, 1957; 1969; 1977; 1988; 1989. <sup>b</sup> Wheat, largely temperate; barley, oats, rye, very largely temperate; maize, about 50% temperate; sorghum and millets, very largely tropical.

distinguishable by morphology and protein electrophoresis (Cook, 1982; Sturhan, 1982b; Rumpfenhorst, 1985). *Heterodera avenae* is the principal species on temperate cereals. *H. latipons*, mainly a mediterranean species, also occurs in northern Europe (Sabova *et al.*, 1988). In semi-arid regions in Cyprus, barley yields were reduced by 50% by *H. latipons* (Philis, 1988). In Israel, *H. latipons* occurred in more arid areas and, unlike *H. avenae*, did not produce knotted roots (Mor *et al.*, 1992). *H. hordecalis* occurs in Sweden, Germany and Britain (Andersson, 1974; Sturhan, 1982a; Cook and York, 1982a). Other gramineous cyst nematodes (Chapter 8, Cook and Yeates) may be found on cereals but have not been shown to be economically significant.

### *Heterodera avenae*

*H. avenae* can be found in all cereal growing areas (Ritter, 1982). It is the most important pathogen of wheat in south eastern Australia, on approximately 1.4 m ha (Brown, 1982a). In Europe more than 50% of fields in major cereal growing areas are infested. In India, it is a severe pathogen of wheat and barley, causing 'Molya disease'. In several states of the USA and in Canada, *H. avenae* is regarded as an important potential pathogen (Miller, 1986). Reports from Japan (Ichinohe, 1954), north Africa and west Asia (Sikora, 1988) confirm that *H. avenae* is likely to be detected wherever its hosts, including some grasses, are widely grown.

Sorghum and  
millets

111

100

98

78

77

0.66

116

137

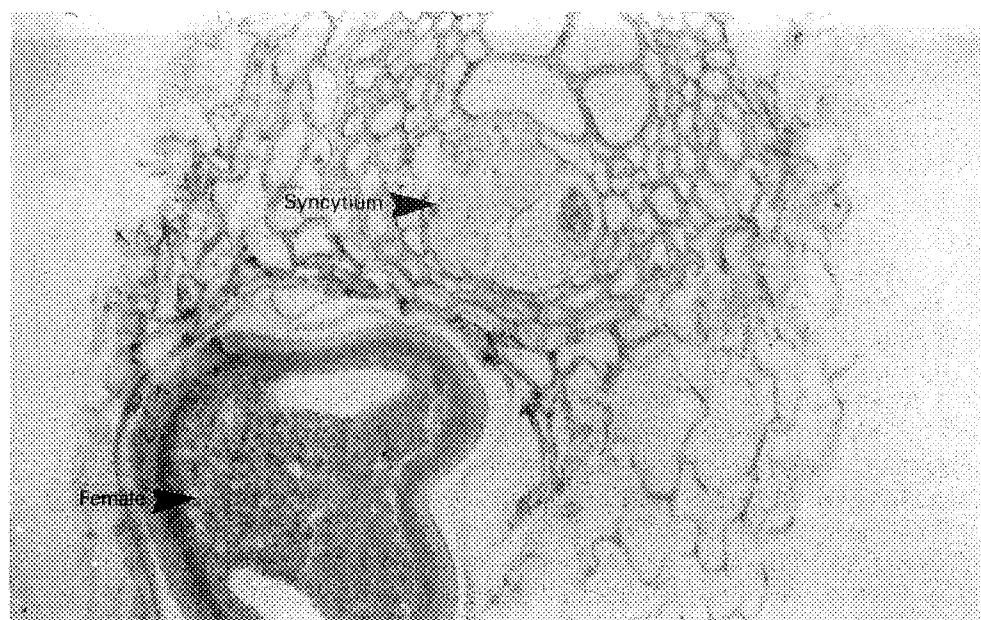
169

168

s, rye, very largely

(Cook, 1982; principal species also occurs in Cyprus, barley and wheat. *H. latipons* produce knotted roots in Cyprus and Britain and other gramineous crops but have

It is the most common pest of cereals, causing damage to approximately 1.4 million ha of major cereal crops in wheat and barley in Canada, *H. avenae* (Cook, 1986). Reports (Cook, 1988) concluding some



**Fig. 7.1.** Transverse section of oat root with cereal cyst nematode *Heterodera avenae* female and syncytium (photo. R. Cook).

### BIOLOGY

*H. avenae* has only one generation a year. Hatch of the second stage juveniles is determined largely by temperature. Juveniles penetrate roots just behind the growing point and pass through cells towards the stele where they induce the development of a feeding syncytium. These 'transport cells' provide food for the development and maturation of females (Fig. 7.1). Adult females are white, lemon-shaped, turning brown after death. The gelatinous matrix exuded around the vulva is always empty of eggs. Males are essential for fertilization.

### SYMPTOMS

In wheat, *H. avenae* stimulates increased rootlet production at invasion sites, so that infested plants have bushy root systems (Fig. 7.2). Individual roots have a knotted appearance, with several females at each knot. Oat roots are shortened and thickened by the parasites (Fig. 7.3). Barley roots are less affected. In fields, attacks are seen as patches of stunted plants, with fewer tillers. Leaf tips often become yellow (barley), red (oat) and reddish-yellow (wheat). Damage is more severe on winter sown soft and durum wheats in mediterranean climates (Australia, southern Europe), and on spring sown crops in temperate oceanic climates (northern Europe).

### ECOTYPES

Hatch of *H. avenae* populations in mediterranean climates is characterized by juvenile emergence from autumn to the beginning of spring (Romero and

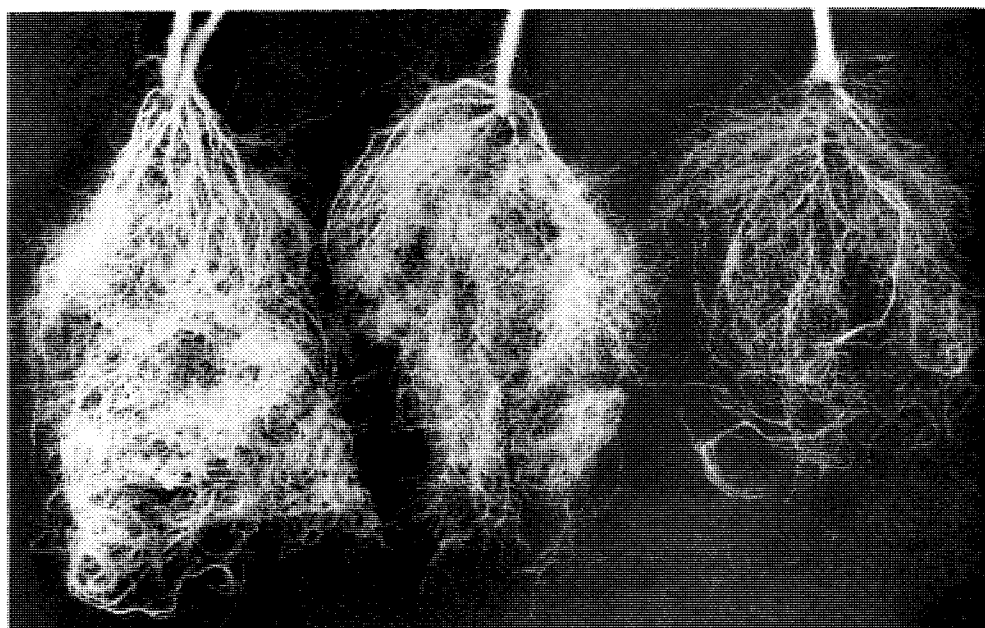


Fig. 7.2. Comparison of effects of *Heterodera avenae* (25 eggs g<sup>-1</sup> soil) on root growth of barley (left), wheat (centre) and oat (right) (photo. R. Cook).

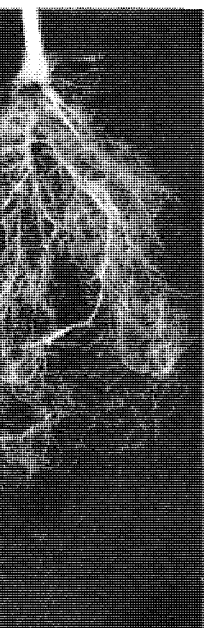
Valdeolivas, 1990). In more northern climes, the majority of juveniles emerge in spring as soil temperatures rise (Rivoal, 1978; Fig. 7.4).

The differences in hatching cycles result from the induction or suppression of dormancy (diapause) by different temperature conditions. In mediterranean climates, the diapause is obligate and durable, acting when hot dry conditions prevail and being suppressed when temperature falls and soil moisture increases. A second diapause may be induced by a temperature rise at the beginning of spring in southern Australia and southern Europe (Banyer and Fisher, 1971; Rivoal, 1979).

In Spain, most populations have winter juvenile emergence, but two populations had a second spring hatch typical of the northern European type (Valdeolivas and Romero, 1986). A southern French population needed 2 months storage at 20°C prior to hatch at 5°C (Rivoal, 1983). Populations from northern Europe have a more facultative diapause from July to the end of winter, which is suppressed by chilling, ensuring emergence of juveniles when soil temperatures increase in spring. Reciprocal transfers of northern and southern European populations did not alter their basic hatching rhythms (Ireholm and Rivoal, 1990).

#### SURVIVAL

Encysted eggs of *H. avenae* survive for several years at 5°C when stored at low relative humidity (Kyrou, 1976; Meagher, 1982b). Wind-borne dispersal of dry cysts accounted for the rapid and widespread distribution of *H. avenae* in Australia (Meagher, 1974). Encysted eggs survive drying in soil without loss of viability and infectivity (Rao and Dhawan, 1988).



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juveniles emerge in

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and soil moisture

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bean type (Valdeo-

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ad Rivoal, 1990).

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borne dispersal of

on of *H. avenae* in

a soil without loss



Fig. 7.3. Cysts and white females of *Heterodera avenae* on oat root (photo. R. Cook).

#### **PATHOTYPES**

A number of pathotypes of cereal cyst nematodes have been recognized using an International Test Assortment of barley, oat and wheat cultivars with resistance genes (Table 7.2). Attempts to characterize some of these pathotypes by isozyme comparisons showed that there was much polymorphism in field populations (Bossis and Rivoal, 1989).

Pathotypes from Sweden and Britain, within the Ha3 group (Table 7.2),



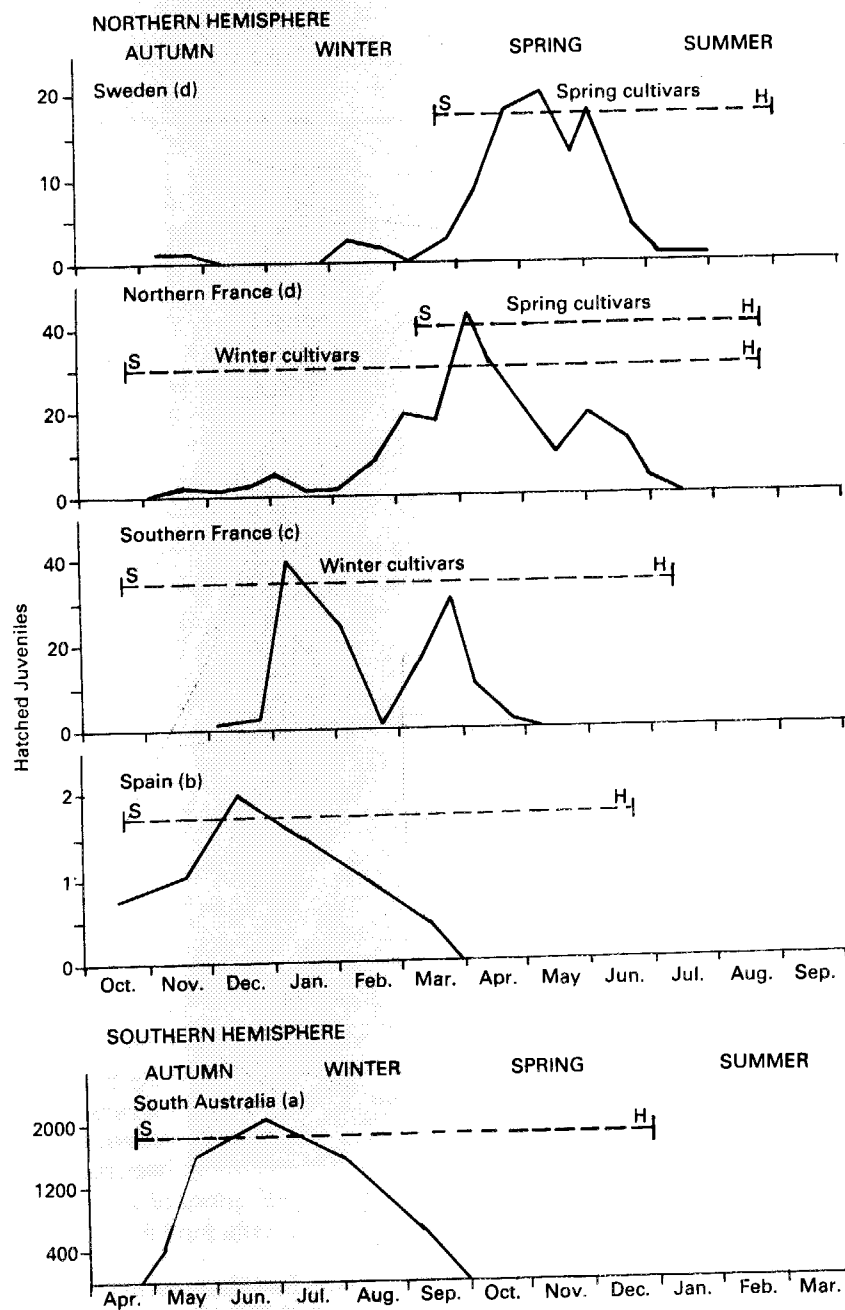


Fig. 7.4. Comparison of hatching patterns of juveniles of *Heterodera avenae* and cropping periods of cereals; sowing (S) and harvest (H) dates (after; a, Meagher, 1970; b, Romero and Valdeolivas, 1990; c, Rivoal, 1978; d, Rivoal and Ireholm, 1990).

were morphologically and biologically different from *H. avenae* (Cook, 1975) and the Swedish populations differed from *H. avenae* in protein constituents (Ferris *et al.*, 1989). Similar populations were found in Bulgaria and in Spain (Valdeolivas and Romero, 1990) and a morphologically similar species from Tadzhikistan was described as *H. filipjevi* (Madzhidov, 1981). There are also pathotypes within Swedish populations of Ha3 morphology, and in *H. hordecalis* (Ireholm, 1990).

In some regions, populations seem to be 'pure pathotypes' with regard to virulence on single defined resistance genes, where either the nematode has been introduced (e.g. New Zealand, Australia, Oregon, USA) or where, in the past, populations have been selected by the growing of cereals with particular resistance genes (e.g. UK, Scandinavia and barley genes Ha1 and Ha2). Other populations have been defined by the frequencies of more than one virulence gene (Person-Dedryver, 1987).

Several populations lack virulence on oats, e.g. from southern France, Spain, Morocco, India, Israel and Japan whereas in much of northern Europe, most oat cultivars are the best hosts of *H. avenae*. Pathotypes have been recognized on oats in Sweden (Ireholm, 1990). The pathotype scheme for a species complex based on interactions with three cereal genera will not easily describe such extensive variations in virulence.

#### POPULATION DYNAMICS

*H. avenae* population development is closely related to quality and frequency of hosts in the rotation. In long term field experiments, multiplication rates were inversely related to initial densities by simple linear regression (Ehrenpfordt *et al.*, 1985; Rivoal and Sarr, 1987) but, on susceptible crops (i.e. most cereals and many grasses) multiplication rate also varied with cereal species, cultivar and soil conditions. At low initial population densities, multiplication rates were less than 10-fold on oats in Sweden (Andersson, 1982) and between 10 and 15-fold on wheat in France (Rivoal and Sarr, 1987). Equilibrium densities showed wide variation, from 2 to 40 juveniles g<sup>-1</sup> of soil on barley in Denmark (Andersen, 1980), 15 to 40 g<sup>-1</sup> on wheat in South Australia (Fisher and Hancock, 1991), and 10 to 100 juveniles g<sup>-1</sup> of soil in different soil and climatic conditions in France (Rivoal and Sarr, 1987).

Under fallow, non-host or resistant cultivar populations decline by 70 to 80% annually by hatching and death of juveniles (Andersson, 1982). In southern France, there was a maximum 42% annual decrease on a non-host crop, very close to the annual hatching capacity of the mediterranean ecotype. Under resistant hosts annual declines may be greater (57–74%) because of the stimulation of hatching by root exudates (Rivoal *et al.*, 1986a).

#### BIOLOGICAL ANTAGONISM

Several fungi, and especially *Nematophthora gynophila* and *Verticillium chlamydosporium* have been associated with widespread decline and suppression of *H. avenae* populations under intensive cereals in northern Europe (Kerry and Andersson, 1983; Kerry, 1987). Induction of suppression may take 5 years,



Table 7.2. Pathotypes of cereal cyst nematodes defined by an International Test Assortment of cereal cultivars<sup>a</sup>.

Pathotype	<i>H. avenae</i> group Ha1 pathotypes										<i>H. hordeocalis</i>		<i>H. bifeneestra</i>
	Ha11	Ha21	Ha31	Ha41	Ha51	Ha61	Ha71	Ha12	Ha13	Ha23	Ha33	Hh1	Hb1
Differential	S <sup>b</sup>	S	-	S	-	R	S	S	S	S	S	S	S
Barley													
Emir [Rha? <sup>c</sup> ]	R	R	R	R	R	R	R	R	R	R	R	R	S
Ortolan [Rha1]	R	R	R	R	R	R	R	R	R	R	R	R	S
Siri [Rha2]	R	R	R	R	R	R	R	R	R	R	R	R	S
Morocco [Rha3]	S	-	R	S	-	S	S	S	S	-	-	-	S
Varde	R	R	-	R	-	S	R	R	R	-	-	-	(R)
KVL191	R	-	R	-	R	-	R	R	R	-	-	-	-
Bajo Aragon	S	S	-	R	-	R	R	R	R	-	-	-	-
Herta	R	-	R	-	R	-	R	R	R	-	-	-	-
Martin 403-2	R	-	-	R	-	R	(S)	R	R	(R)	S	(R)	S
Dalmatische	(R)	-	-	S	-	-	S	S	S	(R)	-	(R)	S
La Estanzuela	-	-	-	-	-	-	S	-	-	(R)	-	-	-
Harlan 43	R	-	-	-	-	-	R	R	-	R	S	-	-

<sup>a</sup>Modified from Andersen and Andersen (1982) and their revision; <sup>b</sup>S<sub>1</sub>, susceptible; R, resistant; ( ) intermediate; - , no observation; <sup>c</sup>resistance genes 1 to 3 in barley defining 3 pathotype groups.

during which time crops may be damaged by the nematode (Kerry, 1987). In experimental rotations dominated by cereals, *N. gynophila*, but not *V. chlamydosporium*, was more common after 3–9 years of susceptible than resistant cultivars (Kerry and Andersson, 1983). *N. gynophila* produces motile zoospores and destroys females whereas *V. chlamydosporium* reduces their fecundity by parasitizing eggs. The degree of suppression by *N. gynophila* was closely related to rainfall and soil moisture in early summer but *V. chlamydosporium*-infections were less dependent on humidity (Kerry, 1982). Whereas in England, eggs were infected by *V. chlamydosporium* in some 13% of cysts, in the drier soils of Australia, the same fungus and *Catenaria auxiliaris* affected only 1% of 23,000 females sampled from 375 sites (Stirling and Kerry, 1983).

#### PATHOGENICITY AND DAMAGE

Degree of damage is determined principally by initial infestation, but is modified by soil and climatic conditions and by crop species and cultivar. Ranges of sensitivity between cereal species and estimates of damage thresholds have been established but have only local relevance. In Australia, yield losses can exceed 50% of the production potential (Meagher, 1982a). Hansen (1986) estimated total losses in barley production of about 30–75,000 tonnes per year in Denmark.

Synchrony of *H. avenae* emergence with cereal sowing time plays a major role in crop damage. In Australia, times of hatching, sowing and rainfall are almost coordinated (see Fig. 7.4), explaining the great losses observed (Georg *et al.*, 1989). There is similar synchrony with winter sown crops in southern Europe. In northern Europe, damage is more frequently observed when wet springs, favouring nematode hatch and invasion, are followed by dry summers (Shiabova, 1982). Barley losses were greater in sandy than sandy loam soils, with losses of 87% grain yield at initial populations of 22 eggs g<sup>-1</sup> soil (Handa *et al.*, 1985). Wheat tolerance was reduced by low Mn concentrations in the soil (Wilhelm *et al.*, 1985). Infested plant roots had restricted ability to forage for phosphate and, in the field in Australia, this was probably the major cause of damage (Simon and Rovira, 1985).

#### CONTROL

*H. avenae* has been economically controlled in Australia with low rates of chemical applied in the drill row at seeding, first with the fumigant, EDB, and later with non-volatile, systemic nematicides (aldicarb, carbofuran). The short delay between application and emergence of juveniles prevented seedling damage and improved crop performance (Brown, 1984b). Similar treatments protected autumn sown wheats from the mediterranean ecotype in the south of France and in other countries with similar climatic conditions (Lacombe and Garcin, 1988; Fig. 7.5).

As a result of its monovoltine nature and relatively low fecundity, *H. avenae* can be managed for successful cereal production by rotations omitting grassy host species. In long term experiments, resistant cereal or non-host crop frequencies of 50% (80% in lighter soils) kept populations below damage thresholds (Rivoal and Besse, 1982; Fisher and Hancock, 1991). Clean fallows

(Kerry, 1987). In not *V. chlamydos-* resistant cultivars the zoospores and fecundity by para- closely related to *sporium*-infections in England, eggs in the drier soils of only 1% of 23,000

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cundity, *H. avenae* s omitting grassy on-host crop fre- below damage 1). Clean fallows



**Fig. 7.5.** Effects of application of aldicarb ( $1 \text{ kg ai ha}^{-1}$ ) on *Triticum durum* on soil infested by *Heterodera avenae*; untreated control with 39 nematodes  $g^{-1}$  root (centre plot) and treated plots (15 nematodes  $g^{-1}$  root) (photo. R. Rivoal).

also control this nematode, but may lead to wind erosion of soil in low rainfall areas.

Some agricultural practices enhance the tolerance of cereals, notably applications of fertilizers (Terenteva and Zhemzchuzina, 1987). In hot climates, repeated deep summer ploughing reduced *H. avenae* incidence in lightly infested soils (Mathur *et al.*, 1987). In Europe, winter barley, as well as suffering little loss, has been recorded as supporting lower population densities than rye, and was recommended as a control crop (Ehrenpfordt *et al.*, 1985).

Cultivar resistance to nematode multiplication is the most promising approach to the control of *H. avenae* (Cook and Evans, 1987). Intensive screening of barley and oat germplasm has identified many sources of resistance genes (Table 7.3).

Landraces are good sources of resistance; thus in north-western Europe oat cv. Sun II was partially resistant (Chew *et al.*, 1981) and many barley cultivars have resistance genes. Resistance has been identified in locally selected barleys in India (Dhawan and Sethi, 1983) and in Spain (Sanchez *et al.*, 1985). Undoubtedly, resistance genes have been dispersed in recent times, by the extensive collection and interchange of germplasm by plant breeders. In wheat, there are several sources of resistance. A single gene from cv. Loros is not effective against pathotypes in every region (Table 7.3). Other sources of resistance in different genomes of related, wild species of *Triticum* may be transferred to *T. aestivum* (Rivoal *et al.*, 1986b; Yu, 1991). The lack of effective resistance in wheat is a major drawback to use of resistance for *H. avenae* control in India.

Table 7.3. Principal sources of genes<sup>a</sup> used in breeding for resistance to *Heterodera avenae*.

Cereal species	Cultivar	Origin	Genetic information <sup>b</sup>	Remarks <sup>c</sup>	Used	Reference <sup>d</sup>
<b>OATS</b>						
<i>A. sterilis</i>	I376	?	1,2 or 3 dom	R, worldwide	UK, Belgium, Australia	1,2,9,11
<i>A. sativa</i>	Panema	UK	1 dom, from I376	S, Australia	UK	4,11
	Nelson	Sweden	1 dom, from C.I. 3444, allelic to Panema	-	N.W. Europe France	2,8,11 23
<i>A. byzantina</i>	N.Z. Cape	New Zealand	?	S, UK	Australia	4,13
	Mortgage Lifter	Australia	2, rec.	-	-	11
	TAMO 301, 302	Texas, USA	?	-	Australia	4
	No 11527	?	?	R, Siberia	-	24
<b>BARLEY</b>						
	many cvs e.g. Emir	N. Europe	?	R, to some pathotypes in many cvs	-	1,2,10
	Drost	Sweden	1 dom ( <i>Rha1</i> )		N. Europe	1,2,10
	Ortolan	Germany	1 or 2 dom, allelic to <i>Rha1</i>			19
	ex. L.P.191	?N. Africa	1 dom, ( <i>Rha2</i> )	many bred cvs	N. Europe	1,2,10
	ex. Morocco	N. Africa	not linked to <i>Rha1</i>	pR, Australia		26
	L.P.191,		1, dom, ( <i>Rha3</i> ) allelic to <i>Rha2</i>	-	Australia	1,2,10,18,26
	Morocco		1-2 dom	-	-	19
	Athenais	Greece	1 dom, not <i>Rha1</i>	-	}	10,26,27
	Nile, C.I. 3576	Egypt	1 dom, similar to <i>Rha2</i>			
	C.I. 8147	Turkey	1 dom, not <i>Rha1</i>			
	Martin	Algeria	2 dom, ?similar to <i>Rha3</i>		Australia	

10,26,27

Australia

1 dom, similar to *Rha2*  
 1 dom, not *Rha1*  
 2 dom, ?similar to *Rha3*

Nile, C.I. 3576  
 C.I. 8147  
 Martin

Egypt  
 Turkey  
 Algeria

## WHEAT

*T. aestivum*

Loros ? 1 dom, Ccn-1 11,14,16,  
 on chromosome 2B 17,22,25

AUS10894 ? Ccn-1 Australia  
 Katiji Australian Ccn-1 14  
 cv

Festiguay Australian Ccn-1 6,20  
 cv

*T. durum*

Psathias ? ? S, to some  
 7654, 7655 ? ? pathotypes  
 Sansome, Khapli ? ? pR 21

*T. ventricosum*

? ? on chromosome 6M<sup>v</sup> 15,21

*T. variable*

? ? on chromosome 3U or 3S<sup>v</sup> 15,28

## TRITICALE

T701 Australia 1 dom, chromosome 6R 3  
 also used in wheat  
 breeding  
 Driva Australia ? =Ningadhu in cv 5,7  
 Tabara  
 Salvo Poland ? UK 12

<sup>a</sup>See also differentials listed in Table 7.4; <sup>b</sup>dom, rec, dominant or recessive genes; <sup>c</sup>R, resistant; pR, partially resistant; S, susceptible; <sup>d</sup>1, Andersen and Andersen, 1986; 2, Andersen and Andersen, 1982; 3, Asiedu *et al.*, 1990; 4, Barr and Dube, 1983; 5, Brouwer, 1989; 6, Brown, 1982b,c; 7, Castleman *et al.*, 1986; 8, Chew *et al.*, 1981; 9, Clamot and Rivoal, 1984; 10, Cook and York, 1982a; 11, Cook and York, 1982b; 12, Cook and York, 1987; 13, Cook and York, 1988; 14, Dhawan, 1988; 15, Dosba and Rivoal, 1981; 16, Fisher, 1982; 17, Nielsen, 1966; 18, Osipova, 1989; 19, Person-Dedryver, 1987; 20, Rathjen *et al.*, 1989; 21, Rivoal *et al.*, 1986b; 22, Rivoal *et al.*, 1991; 23, Saur and Rivoal, 1979; 24, Shiabova and Sheshnikova, 1972; 25, Slocumaker *et al.*, 1974; 26, Soetopu, 1985; 27, Sparrow and Dube, 1981; 28, Yu 1991.



Resistant cultivars have been widely grown in parts of northern Europe and Australia (Andersson, 1982; Brown, 1984a). Five resistant crops in 8 years reduced *H. avenae* to almost undetectable populations (Rivoal *et al.*, 1991). Person-Dedryver (1987) estimated a very low probability of resistance breaking in barley by recombination of different virulence genes.

The roots of resistant cultivars are invaded by juveniles, and some are intolerant of the damage they cause. Characteristics of root growth and their response to invasion both seem to be important in conferring tolerance of damage (Stanton and Fisher, 1988; Volkmar, 1990). In Australia, tolerance has been found in oats and wheats (Stanton and Fisher, 1988; Volkmar, 1989) but oats, resistant and tolerant in Australia, were susceptible and damaged in Britain (Cook and York, 1988). Resistance and tolerance were both recognized in new advanced lines of wheat (Rivoal *et al.*, 1990, 1991).

The obligatory parasitism of the effective biocontrol agent, *N. gynophila* reduces its potential value. In areas where *N. gynophila* is naturally ineffective, attention has focused on *V. chlamydosporium*. This fungus can be cultured but varies greatly in its pathogenicity, rarely affecting more than 50% of eggs in controlled conditions (Irving and Kerry, 1987). None the less, *H. avenae* has been controlled in experiments by introduction of this fungus to Australian soils (Stirling, 1988).

#### DIAGNOSIS AND DETECTION

Suspected *H. avenae* attacks can be diagnosed by staining roots of plants from affected areas to reveal the invaded juveniles. White females can be seen on roots, generally at the flowering stage of the cereal. Precise identification depends on features of cysts and encysted juveniles. Cyst extraction from pre-sowing soil samples can be used to detect potentially damaging populations, subject to local awareness of pathogenicity. Bioassays for pre-sowing assessment of soil infestation and damage potential have been developed in Australia (Simon, 1980) and in Germany (Grosse and Decker, 1983). The Sironem test (a pre-sowing bioassay comparing seedling growth in pouches of nematicide treated and untreated soil) has been used by 1500 growers in the South Australian wheat belt (Baldwin, personal communication).

Remote sensing techniques may detect *H. avenae* attacks on a large scale by observing electromagnetic radiation from plant canopies modified by nematode injuries. Visible and near-infrared images have been used experimentally on highly infested and stunted areas of wheat, barley and oats (Caubel *et al.*, 1978). The thermal infrared (TIR) waveband, responding to disturbances in water relations, allowed early detection of attack (see the frontispiece, Lili *et al.*, 1991).

#### ROOT-KNOT NEMATODES

##### *Meloidogyne naasi*

Cereal root-knot nematode, *M. naasi*, is widely distributed in Europe, apparently

thern Europe and  
crops in 8 years  
Rivoal *et al.*, 1991).  
Resistance breaking

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south of latitude 55°N. It also occurs on small grain cereals in the USA, New Zealand and Chile (Jepson, 1987).

#### SYMPTOMS AND BIOLOGY

*M. naasi* galls range from pea-sized, club-shaped swellings on root tips, to smaller often spindle-shaped intercalary galls. Large galls may contain 100 or more egg-laying females. On severely affected plants, root systems are bushy and shallow and shoot growth is stunted with older leaves yellowing from the tip, and eventually dying (Fig. 7.6). In infested fields, such plants occur in patches (Fig. 7.7).

*M. naasi* generally has one generation per season; spring hatch is synchronized with host root growth, females maturing before grain harvest. The egg masses in galls survive in soil. Eggs require a diapause, broken by rising temperatures, after a cool period (Antoniou, 1989). In warmer regions and on perennial (grass) hosts more than one generation may be completed (Kort,



Fig. 7.6. Barley plant infected by *Meloidogyne naasi* (photo. R. Cook).



Fig. 7.7 Effect of *Meloidogyne naasi* on spring barley sown after a non-host (background) or host (foreground) (photo. R. Cook).

1972). Reproduction is by facultative meiotic parthenogenesis and males are common, especially on poor hosts. Infestations persist for many years; York and Cook (1989) reisolated it from unploughed pasture, 22 years after its initial discovery.

#### ECONOMIC IMPORTANCE AND DAMAGE THRESHOLDS

*M. naasi* caused yield losses in barley in the USA (Allen *et al.*, 1970), France (Caubel *et al.*, 1972), Belgium (Gooris and D'Herde, 1977) and in Great Britain (York, 1980). Wheat is damaged in Chile (Kilpatrick *et al.*, 1976) and Europe; in Italy 17% of durum wheat fields were damaged (Inserra *et al.*, 1978). Severe losses can occur, with whole crops of spring barley having been lost in the Netherlands and France (Schneider, 1967). In California, USA continuous barley cropping led to losses of 50 to 75% (Allen *et al.*, 1970). York (1980) showed that yields of spring barley were reduced by 3.5% for every 10 juveniles  $\text{g}^{-1}$ , up to a maximum 50% loss at 150 juveniles  $\text{g}^{-1}$ . Winter sown barley apparently suffered less damage (Cook *et al.*, 1986).

#### EFFECTS OF ENVIRONMENTAL FACTORS

*M. naasi* damage has been associated with wet and/or over-compacted soils (Franklin, 1973) and damage is not widespread in temperate semi-arid regions (Sikora, 1988). In California, damage occurred on irrigated soils (Allen *et al.*, 1970).

Winter sown barley (Cook *et al.*, 1986) or wheat (Gooris and D'Herde, 1976) supported less multiplication than spring cultivars. *M. naasi* frequently occurs

and may compete with other cereal nematodes, especially *Pratylenchus* spp. (Esmenjaud *et al.*, 1990).

#### HOST RANGE

*M. naasi* reproduces on plants from many families, but Gramineae are the better hosts (Gooris, 1968). Oat is a poorer host than either wheat or barley (Cook, 1972), but Gooris and D'Herde (1972a) noted that oat and some other poor hosts became more susceptible at 25°C. Partial resistance was found in barley, in *T. squarrosa* and *T. monococcum* and full resistance in *H. chilense*, *H. jubatum* and *T. umbellulatum* and *T. variable* (Cook and York, 1982b; Roberts *et al.*, 1982; Person-Dedryver and Jahier, 1985). Resistance from *T. variable* and *H. chilense* have been expressed in bread wheat, providing potentially useful germ-plasm (Person-Dedryver *et al.*, 1990; Yu *et al.*, 1990; Fig. 7.8).

Host races have been identified in the USA on differentials which included crop and weed species (Michel *et al.*, 1973). The identification of resistant cereal relatives provides an opportunity to explore pathotype differences within and between populations.

#### CONTROL MEASURES

*M. naasi* is controlled by rotation with non or poor host crops, e.g. including oats in cereal-grass rotations (Cook *et al.*, 1986; Fig. 7.7). Fallow during the hatching period is also effective (Allen *et al.*, 1970; Gooris and D'Herde, 1972b), but non-hosts such as potato or sugarbeet may be badly damaged by invading juveniles (Gooris and D'Herde, 1972b; Table 7.6).

#### DIAGNOSIS

Field diagnosis may be made by the presence of galls on roots. At planting time, soil populations may be estimated by extraction of juveniles from root and other organic debris or from soil samples. Cold soils should be kept for one week at 20–25°C before extraction, when 90% of juveniles emerge within 5 days. Second stage juveniles are distinguished from other root-knot juveniles by the presence of vesicle-like structures in the median oesophageal bulb, and by their long sharply-pointed tail.

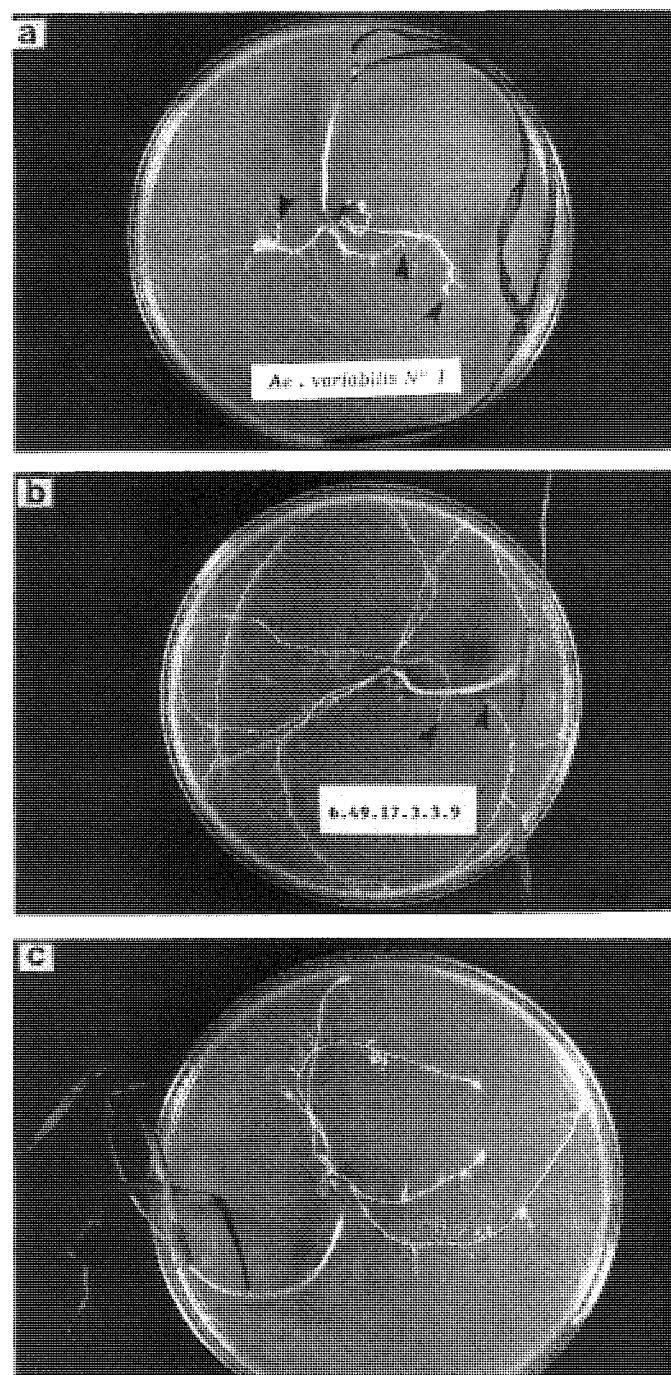
#### *M. artiellia*

*M. artiellia* is known chiefly from Europe, but also west Asia (Sikora, 1988); Syria (Mamluk *et al.*, 1983), Israel (Mor and Cohn, 1989) and western Siberia (Shiabova, 1981).

#### SYMPTOMS AND BIOLOGY

Galls are small, with females only partially embedded. Lateral root proliferation occurs (Franklin, 1961). Females have a unique perineal pattern (Eisenback and Triantaphyllou, 1991). Newly formed eggs require a period of chilling before they hatch (Tobar-Jiminez, 1973). *M. artiellia* is widely adapted, surviving both cold winters and dry summers. Populations fell to 48% in a season when no host was grown (Di Vito and Greco, 1988).





**Fig. 7.8.** Root system 15 days after inoculation with *Meloidogyne naasi*. a) *Triticum variabile*, no galling; b) resistant plant from Chinese Spring x *T. variabile*; c) susceptible *T. aestivum* cv. Lutin with galls. In a and b, arrows mark points of arrested root extension (photo. M.Q. Yu).

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In Italy, cowpea, lupin, sainfoin, and maize were non-hosts, all Cruciferae and most legumes and other families were hosts (Di Vito *et al.*, 1985). In Spain, *M. artiellia* reproduced well in wheat and barley/legume rotations, but poorly on oats; and rye and grasses were resistant (Alcala *et al.*, 1970).

#### ECONOMIC IMPORTANCE AND DAMAGE THRESHOLDS

Damage to wheat occurred in Greece and southern Israel (Kyrou, 1969; Mor and Cohn, 1989). Grain yield losses of 90% occurred at initial population densities of 32 eggs and juveniles  $\text{ml}^{-1}$  soil in microplot experiments with durum wheat in Italy (Di Vito and Greco, 1988).

#### *M. chitwoodi*

*M. chitwoodi* is a major pest in the Pacific North West of the USA and is known also from Mexico, South Africa and Australia (Eisenback and Triantaphyllou, 1991). It has recently been recognized from The Netherlands, where it may have been favoured by a succession of warmer than usual summers (Anon., 1991).

#### SYMPTOMS, BIOLOGY AND HOST RANGE

Females and egg masses are produced outside the galls (Inserra *et al.*, 1985). *M. chitwoodi* is distinguishable morphologically and by the swellings it causes on potato tubers from *M. hapla*, with which it is frequently found (Eisenback and Triantaphyllou, 1991). Wheat, oats, barley, maize and a number of dicotyledons are hosts (Santo and O'Bannon, 1981). Host races were differentiated by the resistance of alfalfa to race 1 but not race 2 (Mojtahedi *et al.*, 1988b).

#### ECONOMIC IMPORTANCE, DAMAGE THRESHOLDS AND CONTROL

*M. chitwoodi* is economically important on potato, but also damages cereals in the USA (Inserra *et al.*, 1985) and Mexico (Cuevas and Sosa Moss, 1990). The tolerance limits, above which damage occurred to wheat sown in pots in February and April, were 0.03 and 0.18 eggs  $\text{ml}^{-1}$  soil and relative minimum yields, proportional to that of uninfested plants and below which no further reduction occurred, were 0.75 and 0.45, respectively (Nyczepir *et al.*, 1984). In the field, winter sown wheat suffered little damage in Utah, USA because invasion occurred some 5 months after sowing, whereas spring sown wheat seedlings were damaged by invasion (Inserra *et al.*, 1985). Several generations of multiplication may occur on small grains, necessitating control measures for potato crops in the rotation.

#### Other *Meloidogyne* spp.

In warm soils (21°C), *M. javanica* reproduced on wheat, but did not when sowing was delayed until soil temperatures had fallen to 16°C (Roberts *et al.*, 1981). In India and Egypt, small grains are damaged by *M. incognita* and/or *M. javanica* (Ibrahim and Rezk, 1988). Host suitability for *M. incognita*, *M. javanica* and *M.*



*arenaria* increased in the order oat < rye < wheat < barley < tomato in experiments in warm soil (Johnson and Motsinger, 1989).

Resistance in wheat, barley, oat and triticale to *M. javanica*, *M. incognita* races 1 and 3, *M. javanica* and *M. arenaria* has been identified (Sharma, 1984a,b,c; Ibrahim and Rezk, 1988). Commercial wheat cultivars in Florida, USA were susceptible, but in practice did not allow population increase of these three *Meloidogyne* species; Florida bred oat cultivars were most resistant (Opperman *et al.*, 1988). The diploid *T. squarrosa* G 3489, has resistance to *M. incognita* races 2 and 3, and to *M. javanica* as well as to *M. chitwoodi* (Kaloshian *et al.*, 1989). Resistance of some barleys, durum wheats and triticales to races of *M. incognita*, *M. arenaria* and to *M. javanica* was not correlated; all accessions were resistant to *M. hapla* (Sasser *et al.*, 1987).

## STEM AND GALL NEMATODES

### *Ditylenchus dipsaci*

Stem nematode occurs as a pest of oats wherever they are grown in Europe, California, USA and Australia.

#### SYMPTOMS, BIOLOGY AND HOST RANGE

Affected plants are stunted, swollen and distorted, with proliferation of tillers, well described by such common names as 'tulip root' and 'poireautage'. Severely infected plants are killed so that infested crops frequently have bare patches (Fig. 7.9)

*D. dipsaci* is a migratory endoparasite, all development stages can invade plants. In good hosts, invading nematodes induce hypertrophy and hyperplasia in parenchymatous tissue, feeding and reproducing for two or three generations. Nematodes from decaying plants spread in soil moisture films, moving as much as 10 cm within 2 h (Kort, 1972). *D. dipsaci* populations persist on many weed hosts, and oat race infestations persisted at least 8–10 years in soil in the absence of crop hosts (Hooper, 1984). Pre-adult juveniles are persistent in soils, and all stages can survive drying within the host.

European cereal races of *D. dipsaci* have many other hosts, including onions and grain legumes (oat race) and oats, maize and grain and forage legumes (rye race). Wheat is attacked by *D. dipsaci* in central and eastern Europe.

#### ECONOMIC IMPORTANCE AND DAMAGE THRESHOLDS

Severe crop damage can result from initially small infestations because many generations can occur on one crop. Damage to oats in microplots occurred when nematode populations at spring sowing were as low as 1 100 g<sup>-1</sup> soil (Wilson and French, 1975). Aldicarb treatment increased yields of spring oat cv. Manod by 37% in field plots with 50–120 *D. dipsaci* 100 ml<sup>-1</sup> soil, and of resistant cv. Maris Tabard by 27% at 110 100 ml<sup>-1</sup>, but not at 50 100 ml<sup>-1</sup> (Whitehead *et al.*, 1983). A decrease of 1 t ha<sup>-1</sup> of spring oat occurred when initial numbers were 150–1500 g<sup>-1</sup> soil (Caubel, 1986).

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**Fig. 7.9.** Effects of *Ditylenchus dipsaci* on growth of susceptible (left) and resistant (right) winter oats (photo. R. Cook).

Weather conditions play a major part in determining the development of damage on infested fields (Seinhorst, 1950). Damage is more severe when soils are moist after sowing, and when low temperatures slow down plant growth and development; winter sown crops therefore suffer more than spring sown ones.

#### CONTROL

The only economic method of control has been the use of host resistance (Fig. 7.9). Most successful winter oats grown in Britain have resistance derived from an old landrace cv. Grey Winter which is also effective in Belgium. The Grey Winter resistance has remained effective for many years in Britain; other sources of resistance are used (Table 7.4).

Oat and rye races are also controlled by growing non-hosts, barley or wheat with strict weed control. Once susceptible oat crops have been damaged, rotation is largely ineffective. In Britain, 20% of oat plants were damaged in a crop sown after three years of barley crops (Wilson and French, 1975).

#### DIAGNOSIS

On oats, *D. dipsaci* symptoms are characteristic although some other pests cause superficially similar symptoms (e.g. frit fly, *Oscinella frit* L. and oat spiral mite, *Steneotarsonemus spirifex* March.). Suspect plants should be teased apart in water at a microscope to confirm the presence of reproducing *D. dipsaci*.

**Table 7.4.** Source of resistance to stem nematode (*Ditylenchus dipsaci*) in oats and rye.

Crop species	Cultivar	Remarks <sup>a</sup>	Reference
<i>Avena sativa</i>	cv. Grey Winter UK winter cvs <sup>b</sup> Belgian spring cvs <sup>b</sup>	1 dom, HR	Griffiths <i>et al.</i> , 1957 Goodey and Hooper, 1962 Cook and Evans, 1987 Clamot, 1985
	Early Miller		Cameron and Speed, 1958
<i>A. sativa</i> x <i>A. byzantina</i>	Uruguayan landrace Victoria <sup>b</sup> Manod <sup>b</sup>	R	Goodey and Hooper, 1962 Whitehead <i>et al.</i> , 1983 Blake, 1962
<i>A. byzantina</i>	USA cvs Curt, Moregrain	R/T	Radewald <i>et al.</i> , 1971
	Australian cvs Algerian, Avon, Cassis	R/T	Stanton <i>et al.</i> , 1984
<i>A. ludoviciana</i>	Cc4346, 4347	2 genes, HR	Griffiths <i>et al.</i> , 1957
<i>Secale cereale</i>	NL, Landrace	HR	Poos, 1956

<sup>a</sup>dom, dominant gene; HR, hypersensitive resistance; R, quantitatively expressed resistance; T, tolerance through rapid stem elongation and tissue differentiation; <sup>b</sup>cvs derived by hybridization and/or selection.

### ***Anguina tritici***

Seed gall nematode is frequently found on small grain cereals where farm saved seed is sown without modern cleaning systems. Wheat is infested throughout temperate semi-arid north Africa and west Asia (Sikora, 1988). It is also a problem in the Indian sub-continent, in China and parts of eastern Europe (Tesci, 1969; Swarup and Sosa-Moss, 1990).

#### **SYMPTOMS AND BIOLOGY**

Shoots and leaves of infected plants are distorted, but characteristically ovules and other floral parts are transmutated into galls. Second stage juveniles can survive in dry galls for many years.

Invasive juveniles from moistened galls infect stem growing points and are carried with the embryonic ear by stem elongation. Mating and egg laying occur within the gall. Infection is greatest when growing conditions include cool periods with higher moisture levels. *A. tritici* is spread with infested seed.

Wheat and rye are attacked, and although barley is not commonly affected in India, this was attributed to the crop being grown on arid lands (Paruthi and Gupta, 1987). In Iraq, barley was attacked by an isolate which did not infect wheat (Al-Tabib *et al.*, 1986). Oat, maize and sorghum were not hosts (Limber, 1976; Paruthi and Gupta, 1987).

#### **ECONOMIC IMPORTANCE AND DAMAGE THRESHOLDS**

Individual crop losses of up to 60% or more occur when infested seed is sown

(Chu, 1945; Al-Beldawi *et al.*, 1974; Paruthi and Bhatti, 1985). The bacterium *Corynebacterium michiganense* pv. *tritici* causes yellow ear rot when associated with *A. tritici*. Economic loss is increased because of the lower price for infested grain.

#### CONTROL

*A. tritici* is simply controlled by sowing clean, non-infested seed, using modern seed cleaning techniques or simply removing galls by sieving and freshwater flotation (Singh and Agrawal, 1987). In infested areas, rotations should exclude cereals in the preceding growing season. Resistant wheat cultivars have been identified in Iraq (Saleh and Fattah, 1990), Pakistan (Shahina *et al.*, 1989) and resistance is being bred for in India (Swarup and Sosa Moss, 1990).

#### DIAGNOSIS

Infestation can be detected by examination of seed lots for galls, and soaking these in water to confirm nematode infestation; crop infestations can be recognized by plant symptoms, and by teasing apart infested plants. Unlike *D. dipsaci*-infected plants, these do not show tiller proliferation.

#### *Subanguina radicicola*

*S. radicicola* attacks roots of Gramineae in northern Europe, Russia and North America (Kort, 1972). Galls are large and there are relatively fewer per root system than those of *M. naasi*. Root staining of suspected plants confirms which nematode is present. *S. radicicola* seems to be of no economic importance on cereals.

#### OTHER ROOT PARASITES

##### *Pratylenchus* spp.

At least eight species of root lesion nematodes, *Pratylenchus*, have been recorded on small grains. Their identification is rather difficult, and based on tenuous morphological features (Loof, 1978).

#### SYMPTOMS

In infested fields, stunted and chlorotic plants occur in large patches (Fig. 7.10). Roots are irregularly swollen, with necroses from extensive destruction of cortical cells by nematode feeding and migration.

#### PATHOGENICITY AND DAMAGE THRESHOLDS

High numbers of *Pratylenchus* are frequently associated with poorly growing cereals but data on damage are sparsely, though widely distributed (Table 7.5). In dry areas, damage was more severe to early sown crops, possibly



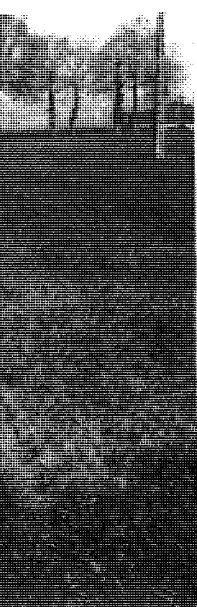
Fig. 7.10. Winter wheat attacked by *Pratylenchus neglectus* (photo. R. Rivoal).

because of greater nematode activity when soil temperatures were higher (Van Gundy *et al.*, 1974). *P. thornei* and *P. minyus* (= *neglectus*) infestations were concentrated in seminal roots and disturbed water absorption efficiency. *P. thornei* was most prevalent and limited wheat yield in fallow treatments designed to conserve soil moisture (Marley and Littler, 1989). *P. thornei* root populations were greater from dry land plots ( $300 \text{ g}^{-1}$  fresh weight) than in irrigated plots and caused greater yield losses (Orion *et al.*, 1984). In northern Europe, early infestations in autumn seem to be responsible for *Pratylenchus* injuries on young roots of winter barley and wheat; *P. crenatus* and *P. penetrans* are particularly damaging in low pH soils (Marzin and Rivoal, unpublished). *P. penetrans* control by aldicarb gave wheat grain yield increases of 10–19% (Kimpinski *et al.*, 1989). *Pratylenchus* spp. infestations of  $380 \text{ g}^{-1}$  root and  $230 \text{ 100 ml}^{-1}$  soil, had no effects on dry matter yields of oat grown for forage, possibly because there was no other applied stress (Yeates and Hughes, 1990).

#### POPULATION DYNAMICS

*Pratylenchus* spp. have several generations per year and can develop large populations under cereals (Esmenjaud *et al.*, 1983, 1990). Populations are strongly influenced by soil characteristics (Kort, 1972). Wheat monoculture with straw ploughed into soil supported significantly fewer *Pratylenchus* spp. than when straw was removed and populations stayed at an almost undetectable density in competition with *M. naasi* (Esmenjaud *et al.*, 1990). *P. neglectus* increased and became predominant on plots previously cropped with cultivars resistant to *Heterodera avenae* (Cotten, 1970; Rivoal and Lasserre, unpublished). Intensive maize cropping in temperate west Europe was responsible for





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**Table 7.5.** Estimates of pathogenicity of root lesion nematodes (*Pratylenchus* spp.) to temperate small grain cereals.

Nematode	Cereal	Experimental conditions	Population density in untreated control <sup>a</sup>		Plant response <sup>b</sup>	Country	Reference
			At sowing	At harvest			
<i>P. thornei</i>	wheat	fumigant; field	—	100 g <sup>-1</sup> root	+70% grain wt	Israel	Orion <i>et al.</i> , 1984
<i>P. thornei</i>	wheat	MBr fumigant; field	—	1660 100 ml <sup>-1</sup>	+78% grain wt	Australia	Doyle <i>et al.</i> , 1987
<i>P. thornei</i>	barley	MBr fumigant; field	—	540 100 ml <sup>-1</sup>	NS grain wt	Australia	Doyle <i>et al.</i> , 1987
<i>P. thornei</i>	wheat (7 cvs)	aldicarb; field	—	120 100 ml <sup>-1</sup> (to 10 cm)	+27% grain wt	Australia	Doyle <i>et al.</i> , 1987
<i>P. thornei</i>	barley	aldicarb; field	—	4 100 ml <sup>-1</sup> (to 10 cm)	+10% grain wt	Australia	Doyle <i>et al.</i> , 1987
<i>P. thornei</i>	wheat	pots	670 100 ml <sup>-1</sup>	—	-24% fresh wt	USA	Mojtahedi <i>et al.</i> , 1988a
<i>P. thornei</i>	wheat	field observations	50–100 100 ml <sup>-1</sup>	—	damage threshold	Mexico	Van Gundy <i>et al.</i> , 1974
<i>P. thornei</i>	wheat	pots	42 100 ml <sup>-1</sup>	—	-26% ear wt	Mexico	Van Gundy <i>et al.</i> , 1974
<i>P. thornei</i>	wheat	pots	420 100 ml <sup>-1</sup>	—	-45% ear wt	Mexico	Van Gundy <i>et al.</i> , 1974
<i>P. crenatus</i>	spring barley	field	—	500 g <sup>-1</sup> root	yield neg. correlated with Pi	France	Bocquet, 1975
<i>P. fallax</i>	spring wheat	field	—	2000 g <sup>-1</sup> root	yield neg. correlated with Pi	France	Bocquet, 1975
<i>P. neglectus</i>	spring barley	pots	150 100 ml <sup>-1</sup>	—	-9% grain wt	Poland	Wolny, 1989
<i>P. penetrans</i>	wheat	aldicarb; field	—	—	+10–19%	Canada	Kimpinski <i>et al.</i> , 1989

<sup>a</sup>Nematodes 100 ml<sup>-1</sup> soil or g<sup>-1</sup> root; <sup>b</sup>(treatment × 100/control) — 100



the establishment of population densities of *P. penetrans*, *P. crenatus* and *P. fallax* damaging to winter wheat and barley (Marzin, personal communication).

#### CONTROL

Effective broadcast applications of nematicides were uneconomic for small grains (Van Gundy *et al.*, 1974). There is some promise in strategies using seed dressings of systemic carbamates (Orion and Shlevin, 1989). The best solutions are to manage rotations with poor hosts, e.g. beet and oat against *P. crenatus* (Townshend, 1989); beet crops are frequently recorded as poor hosts for a number of species (Esmenjaud *et al.*, 1990). Rape controls *P. thornei* and *P. crenatus* (Scotto la Massèse *et al.*, 1981). Fallowing caused 90% mortality of *P. thornei* after 2 years in Israel (Orion *et al.*, 1984). Resistance has not been found in small grains, although tolerance varied in oat and wheat cultivars (Townshend, 1989; Table 7.6).

#### Other nematodes

Different root parasitic genera (*Helicotylenchus*, *Tylenchorhynchus*, *Merlinius*, *Belonolaimus*) have been reported to cause losses to small grain production in specific regions of India, USA and Europe. *Longidorus belloii* induced galls on the root tips of wheat and barley (Andres *et al.*, 1989). In England, *L. elongatus* and *L. leptocephalus* each reduced spring barley yields by more than 2 t ha<sup>-1</sup> for every 100 nematodes 100 g<sup>-1</sup> soil (Brown and Sykes, 1975; Sykes, 1979). Boag *et al.* (1990) suggested that combined populations of *Pratylenchus*, *Tylenchorhynchus*, *Helicotylenchus*, with *Longidorus* and *Trichodorus*, caused yield losses in Scotland.

#### Maize and Sorghum

*Zea mays* is widely distributed but more prevalent in warm temperate areas. In industrialized countries, maize is used for livestock feed and as raw material for many industrial products. Specific cultivars serve special needs, e.g. sweet corn and corn oil. In contrast to maize, *Sorghum vulgare* is less demanding of fertilizer and water supplies and is particularly adapted to dry regions, where it is used largely for animal feed although it can serve for human food (Moule, 1980).

#### CYST NEMATODES

##### *Heterodera avenae*

*H. avenae* damage to maize has been reported in Canada and Europe, with yield losses up to 50% (Hirling, 1984). Damaged plants are stunted, reddish or yellowish with poorly developed seminal roots. The most severe losses were

*crenatus* and *P. fallax* (communication).

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Table 7.6. Yield responses and host status of crops to cereal nematodes in Europe<sup>a</sup>.

Species	Wheat	Barley	Oat		Rye	Maize		Beet	Clover Lucerne	Rape
			North	South		North	South			
<i>H. avenae</i>	xxx <sup>b</sup>	xxx <sup>c</sup>	xxx <sup>c</sup>	x	x	xxx <sup>c</sup>	-	-	-	-
<i>M. naasi</i>	++	++ <sup>c</sup>	++ <sup>c</sup>	+	+	+	-	-	-	-
<i>M. artiellia</i>	xx	xxx	xxx	+	xxx	+	xx	x	-	-
	++	++	++	+	++	+	-	-	-	-
<i>P. crenatus</i>	xxx	xxx	xxx	++	/	/	/	/	/	xx
	++	++	++	+	+	+	+	+	+	++
<i>P. penetrans</i>	xx	xx	xx	++	-	-	xxx	-	xx	+
	++	++	++	+	xx	xx	++	-	++	xx
<i>P. fallax</i>	xx	xx	xx	x	++	++	xx	-	xx	++
	++	++	++	+	/	/	xx	-	++	++
<i>P. thornei</i>	xx	xx	xx	xx	/	/	xx	-	-	x
	++	++	++	++	/	/	++	-	-	+
<i>P. neglectus</i> (= <i>minutus</i> )	xx	xx	xx	xx	/	/	x	x	/	xx
	++	++	++	+	/	/	+	-	/	++
<i>D. dipsaci</i>	-	-	-	xxx	xxx	xxx	xxx	xxx	xxx	x
	-	-	-	++	++	++	-	++	++ <sup>d</sup>	+

<sup>a</sup>(After Esmenjaud *et al.*, 1983, 1990; Decker, 1989; Wolny, 1989; Marzin, personal communication). <sup>b</sup>Levels of: yield loss: xxx, severe; xx, moderate; x, little; -, none; /, no observation. <sup>c</sup>host status: ++, very susceptible; ++, moderately susceptible; +, resistant; -, immune; /, no observation. <sup>d</sup>Variations according to the ecotype and the pathotype concerned. <sup>e</sup>Specialized race attacking only maize.

observed in the 1970s when maize growing was extending into northern Europe, where peak juvenile emergence coincided with spring sowing times (Rivoal, 1982).

Maize is resistant to *H. avenae*, reacting hypersensitively, and young plants are intolerant of invasion damage. Juveniles can develop in maize but few form gravid cysts (Rivoal, 1975). Low rates of carbamates in the seed bed protected seedlings (Rivoal *et al.*, 1981). Similar control was obtained with 2 years previous cropping with resistant oats (Rivoal, 1986). *H. avenae* did not develop cysts on sorghum (Sabova *et al.*, 1987).

### ***Heterodera zae***

Corn cyst nematode (Golden and Mulvey, 1983) has been recorded from cereal growing regions of India, Pakistan, Egypt and the USA (Aboul-Eid and Ghorab, 1981; Sardanelli *et al.*, 1981; Sharma *et al.*, 1984; Ahmed and Qasim, 1990).

### **BIOLOGY**

In the USA and Egypt, the host range of *H. zae* is limited to Gramineae, although it has been associated with non-Gramineae from field records elsewhere (Baldwin and Mundo-Campo, 1991). On maize development was quickest at 32°C, juveniles failed to develop on wheat at either 15 or 23°C but did at 32°C, when there were more males and intersexes than on maize (Bajaj *et al.*, 1986). Optimal temperature for emergence was 25°C and for reproduction, about 30°C (Hutzell and Krusberg, 1990), limiting its impact to warm temperate areas.

### **PATHOGENICITY AND CONTROL**

*H. zae* is of little or no economic importance in the USA where infestations of up to 120 cysts 100 g<sup>-1</sup> soil occur (Krusberg, 1988). In pots, damage thresholds of two Indian populations were 100 and 1000 juveniles g<sup>-1</sup> soil (Srivastava and Sethi, 1984).

Some maize cultivars have moderate resistance in India (Shahina *et al.*, 1989). Kheir *et al.* (1989) separated four Egyptian populations into three distinct groups based on the reaction of differentials selected from 15 maize cultivars. The management of *H. zae* and other diseases of maize was reviewed by Kaiser (1986). In Maryland, USA, areas infested by *H. zae* have been quarantined since 1984 (Baldwin and Mundo-Campo, 1991).

### ***Heterodera sorghii***

*H. sorghii* was reported in India from soil around poorly growing sorghum and peanut (*Arachis hypogaea*) (Sakhuja and Singh, 1985; Sharma and Sharma, 1988). Some variation in cultivar response has been reported by Srivastava and Sethi (1988).

## ROOT-KNOT NEMATODES

### *Meloidogyne* spp.

In warmer temperate regions, maize is liable to attack by *M. incognita*, *M. javanica* and *M. arenaria*, and *M. incognita* is recorded on maize from several European countries (Hirling, 1984). Maize is a non-host of *M. hapla*, probably contributing to its control in much of north central USA (Norton, 1984), and a poor host of *M. naasi* (Hirling, 1984).

Sorghum is attacked by *M. incognita* and by *M. acronea* in South Africa, and by *M. naasi* in Kansas, USA and Thailand (Frederiksen, 1986).

### HOST STATUS

Although maize has frequently been included in rotations to control *Meloidogyne* species, many maize hybrids are hosts and of limited value for root-knot control (Windham and Williams, 1988). However, in Zimbabwe, the level of reproduction of *M. incognita* and *M. javanica* on maize did not jeopardize its use in rotations with more susceptible crops (Way and Shepherd, 1986). Improved levels of resistance have been identified to *M. javanica* (Al Hazmi, 1988; Brito and Antonio, 1989). Maize accessions resistant to *M. arenaria* in Mexico were susceptible to both *M. incognita* and *M. javanica*, whereas in Mississippi, USA, resistance to *M. arenaria* and *M. javanica* were correlated, but that to *M. incognita* was independently transmitted (Sasser *et al.*, 1987; Williams and Windham, 1990).

Sorghum was a poor host of *M. incognita* (Orr and Morey, 1978) and of *M. javanica* and *M. arenaria* races 1 and 2 (Fortnum and Currin, 1988).

### ECONOMIC IMPORTANCE AND DAMAGE THRESHOLDS

In the USA, maize growth was retarded by more than 4 eggs ml<sup>-1</sup> soil of *M. incognita* (Barker and Olthoff, 1976). In pots in Italy, 10 *M. incognita* eggs g<sup>-1</sup> soil was the tolerance limit for maize; at 1000 eggs g<sup>-1</sup>, the yield was only 10% that of nematode-free controls (Di Vito *et al.*, 1980). In the field, growth and yield of maize were not inversely correlated with pre-plant populations of *M. incognita* (McSorley and Dickson, 1989) and in pots, *M. javanica* only slightly galled maize and did not affect growth (Shepherd, 1986).

Sorghum is regarded as more tolerant of stress, including that imposed by nematodes (Dunn, 1988). Nevertheless, *M. incognita* reduced yields by 15% (Orr and Morey, 1978) and *M. naasi* caused severe stunting (Aytan and Dickerson, 1969).

### DIAGNOSIS

As infected maize and sorghum roots are often not markedly galled, staining to confirm infestation is recommended (Swarup and Sosa-Moss, 1990).

## STEM NEMATODE

### *Ditylenchus dipsaci*

Maize is a poor host of stem nematode, *Ditylenchus dipsaci*, in northern Europe, but populations from other rotational crops can cause damage in northern Europe (Hirling, 1984). Losses can be very great as individual maize plants die or fall over before harvest (Fig. 7.11). Damage results from the necrotic reaction to invasion of stem tissues of young plants, and was greater at 15°C than 20–25°C (Caspary, 1976). Early sown crops were more affected than later sowings, when as few as 2 or 3 nematodes per plant caused severe damage.

Stem nematode populations declined by 50% under maize (Caubel, 1986) and the incidence of *D. dipsaci* has decreased as the maize area has increased. Avoiding good hosts (beans, field peas) and rotations with resistant oat and weed free non-host barley are advised for control (Caubel, 1986). Aspects of chemical control are the same as for *H. avenae* (Caubel and Rivoal, 1977).

## OTHER ROOT PARASITES

### *Pratylenchus* spp.

Species most frequently associated with poor growth of maize and sorghum are *P. zeae*, *P. scribneri* and *P. hexincisus*, principally in the USA, South Africa and India.

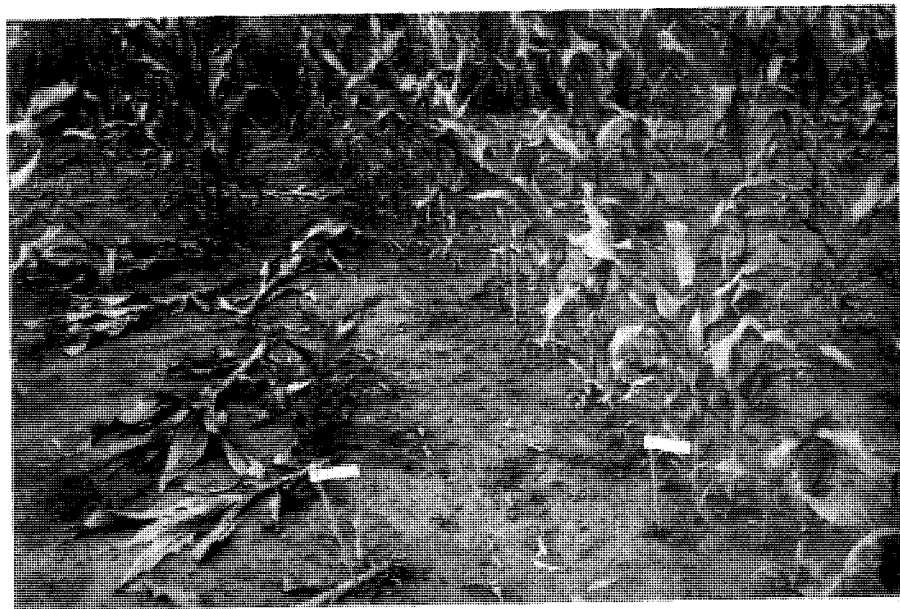


Fig. 7.11. Toppling of maize by *Ditylenchus dipsaci* after early sowing (left) or late sowing (right) (photo. G. Caubel).

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### PATHOGENICITY

Damage is non-specific resulting in stunted and chlorotic plants in field patches. Sorghum roots showed necrotic lesions with varying extension according to the reactions of host species or cultivars (Motalaote *et al.*, 1987). Mid-season infestations of 3400 *P. hexincisus* g<sup>-1</sup> dry root reduced yields of dryland maize in South Dakota, USA by 0.6 t ha<sup>-1</sup>, whilst in irrigated maize, 8200 *P. scribneri* g<sup>-1</sup> root caused a 0.3 t ha<sup>-1</sup> loss (Smolik and Evenson, 1987). *P. zae* is a potential pathogen of sorghum but pathogenicity was greatly affected by environmental conditions (Motalaote *et al.*, 1987). In South Africa and Germany, rainfall and lower temperature during the establishment of maize enhanced the pathogenicity of *P. zae*, *P. brachyurus* and *P. crenatus* (Homeyer, 1985; McDonald *et al.*, 1987).

### POPULATION DYNAMICS

High inputs allow continuous maize cropping for several years, resulting in damaging densities of *P. fallax*, *P. crenatus* and *P. penetrans* in parts of France (Caubel *et al.*, 1980). In Pakistan, growing wheat followed by three maize crops favoured highest numbers of *P. zae*, causing visible injury to maize (Maqbool and Hashmi, 1986). Densities of *P. brachyurus* were positively correlated with increasing annual rainfall, and those of *P. penetrans* to both rainfall and sand content (Jordaan *et al.*, 1989).

Sorghum (cv. Pioneer 8222) was susceptible to lesion nematodes in the USA but host status differed for different species (Motalaote *et al.*, 1987). The association of lesion nematodes and fungi in root rots is controversial. In South Africa, there was synergism in damage to maize between *P. brachyurus*, *P. zae* and *Fusarium moniliforme* (Jordaan *et al.*, 1987). In Nigeria, *P. scribneri* enhanced the invasion of *Helminthosporium pedicellatum* with subsequently increased root rot severity and reduced maize yield (Egunjobi *et al.*, 1986). Chambers (1987) found no significant correlations between *Pratylenchus* spp. and such fungi.

### CONTROL

Practically, control relies on avoidance of susceptible hosts in the rotation. In greenhouse and field, sources of resistance were found in *Z. mays* and related species (*Z. diploperennis* and *Z. perennis*) to *P. brachyurus*, *P. hexincisus* and *P. zae* in Brazil and in the USA (Lordello *et al.*, 1985; Norton, 1988). Two dominant genes in line Col 2(22) conferred resistance to *P. zae* and *P. brachyurus* (Sawazaki *et al.*, 1987). Partial resistance to *P. hexincisus* and *P. scribneri* has been identified (Smolik and Wicks, 1987). Maize inbred lines varied as hosts of *P. scribneri*; those which supported greatest numbers had reduced root size, whilst the most resistant inbreds had no visible root symptoms (Waudou and Norton, 1986).

### Other nematodes

#### DAMAGE

Many migratory parasites are associated with maize and sorghum crops.



Damage by increasing densities of *Tylenchorhynchus mashhoodi* on maize and *Helicotylenchus dihystra* on sorghum was demonstrated in India (Mahapatra and Das, 1984; Jain and Hasan, 1987). Control of *T. dubius*, which multiplied four fold in untreated plots, increased maize dry matter yields in England by up to 37% (Williams and Beane, 1984). In the USA, *Belonolaimus longicaudatus* depressed maize yields but effects varied from year to year (McSorley and Dickson, 1989). Damage was seen as general stunting, fewer tillers and discoloration of foliage.

Concomitant species of ectoparasites cause damage. *B. longicaudatus* and *Dolichodorus heterocephalus* in the USA reduced maize yields in spite of interspecific competition (Rhoades, 1985). *Quinisulcius acutus* and *Pratylenchus zeae* were partly responsible for sorghum decline in Mississippi, USA (Cuarezma-Teran and Trevathan, 1985). In the Netherlands, nematicides which controlled both *Pratylenchus* and *Tylenchorhynchus* improved early plant growth, but failed to increase final yields (Scholte and s'Jacob, 1983). *T. nudus* and *Trichodorus allius* reduced sorghum growth (Smolik, 1977).

#### CONTROL

Nematicide application combined with sub-soiling controlled *B. longicaudatus*, *Hoplolaimus galeatus* and *Trichodorus christiei* for up to 2 years of maize cropping (Rich *et al.*, 1985). In spite of economical and ecological constraints, low applications of nematicides protect maize from the majority of pathogenic ectoparasitic nematodes (Dickson and Hewlett, 1987; Johnson and Wright, 1988).

### Conclusions: Economics and Prospects

Over many centuries, cereal growing has evolved in conjunction with cereal nematodes to produce relatively stable production systems. Recent technological changes have solved some persistent nematode problems but intensified others. In temperate zones, cereal growing faces three challenges: (i) managing excess production in industrialized countries; (ii) maintaining profitability despite increasing costs of inputs and falling grain prices; and (iii) safe-guarding the environment from effects of excessive fertilizer and pesticide usage in intensive cereal production.

Cereal nematodes which cause average losses ranging from 5 to 10% (Sasser, 1989) will continue to be vital factors in the real economics of cereal production. Research in the last 20 years has demonstrated the impact of many nematode species. In low value cereal production, economic control will be achieved only by integrated management, including crop rotation, using high quality resistant and tolerant varieties, and perhaps incorporating applications of synthetic or biological nematicides. Nematicides with persistent effects must not leave toxic residues.

Future studies are likely to emphasize interactions between parasites and

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the effects of these on their host inter-relationships; and to focus on the genetics of virulence/resistance interactions. Biological antagonists will be intensively evaluated for their own potentialities and those of their produced toxins. Molecular and cell biology technologies could find pertinent applied models in cereal nematode interactions, for the manipulation of adverse genes in the hosts and could create new control tools against these parasites.

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