STUDIES IN THE HOST/PARASITE RELATIONSHIP BETWEEN MEMBERS OF THE GENUS *SOLANUM* AND EELWORM, *HETERODERA ROSTOCHIENSIS* WOLLENWEBER.

THESIS

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PUBLICATIONS

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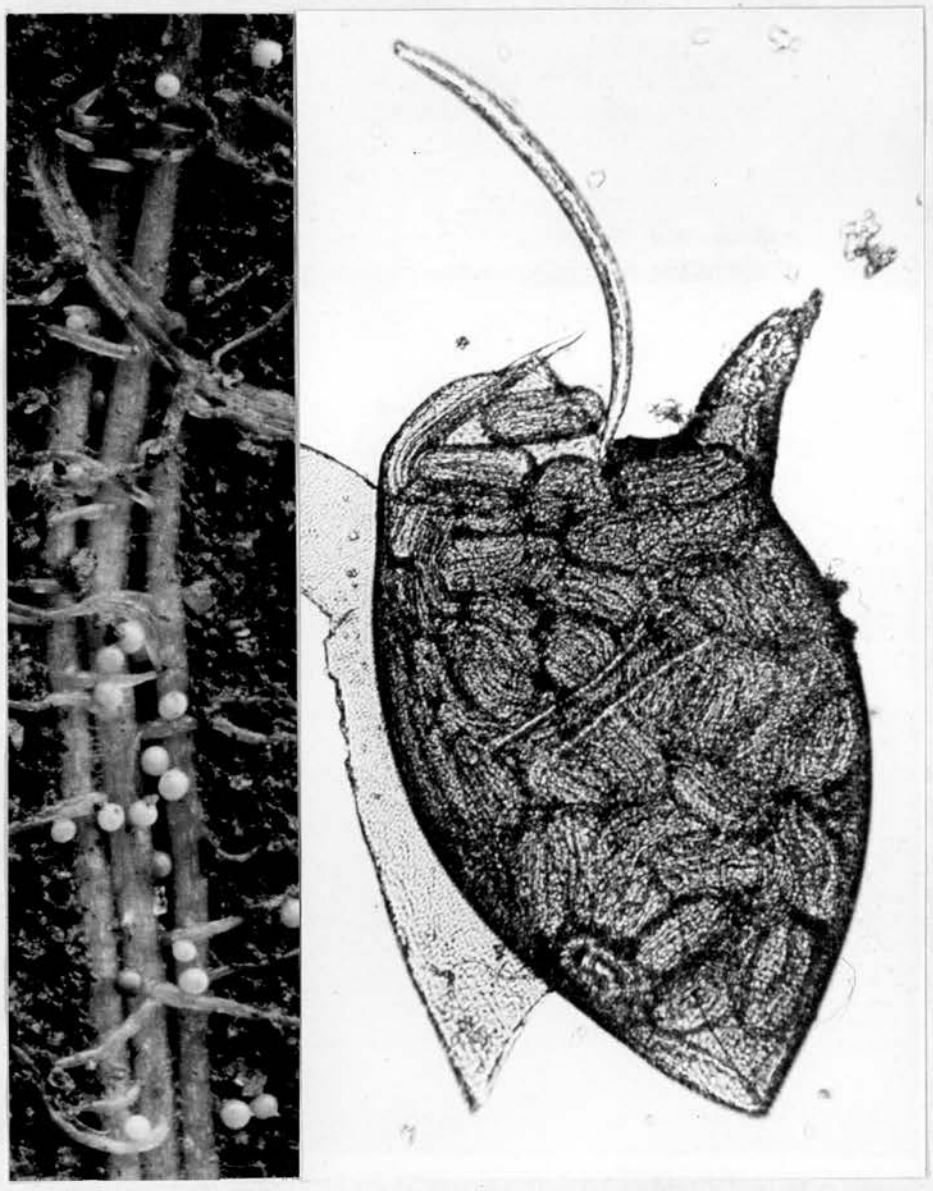
SECTION II, modified version published under the same title - Deutsche Akademie der Landwirtschaftswissenschaften zu Berlin, 20, 107-120 (1958).

SECTION III, published under the same title - Nematologica, (Suppl.II)., 84-94 (1960).

SECTION IV, published under the same title - Rep. Scot. Pl. Breed. Sta., 39-44,(1960).



(a) (b)

Frontispiece: (a) Cysts of Heterodera rostochiensis in situ on potato roots.

(b) Eggs visible through the wall of a cyst crushed in water, and invasive larvae emerging. (Greatly enlarged).

GENERAL INTRODUCTION:

PROBLEMS OF CONTROLLING POTATO ROOT EELWORM

The economic importance of potato root eelworm dates from 1913 when potatoes growing near Rostock in East Germany were seen to be damaged by the pest. Today, the pest can be found in the main potato-growing areas of most West European countries and was responsible in Britain alone in 1949 for an estimated loss of yield amounting to 200,000 tons of potatoes, worth about £2,000,000. No visible damage is done to the tubers by potato root eelworm. The pest also attacks the roots of tomatoes. All other crops and all the common weeds are immune.

Certain factors in the life cycle make the pest very difficult to control. Firstly, the eggs are retained in the dead body of the female which forms a tough-walled cyst. (Frontispiece). This, and the fact that the cysts may be deeply buried, tends to protect the eggs from the effects of nematicidal chemicals applied to the soil. Chemical control in the field is uneconomic at present, but further research may result in better nematicides and better techniques for applying them.

Secondly, cysts that have been in the soil from ten to twenty and possibly even thirty years, depending on conditions, may still contain eggs that will hatch under the stimulus of the hatching factor which diffuses from potato roots. Therefore, the time required to "starve out" the pest by with holding potato crops is inconveniently long. On the other hand, an interval of four years between potato crops is probably enough to prevent a progressive increase

in the infestation of the soil and further reductions in yield, but only if "volunteer potatoes" are prevented from growing as weeds in cereal or other crops succeeding potatoes in rotation.

In theory, resistant varieties of potato provide a means of extending the "starving out period" without extending the interval between potato crops. For example, take three potato crops with an interval of five years between them. If the second crop is a resistant variety on which virtually no new cysts appear, the "starving out period" is increased from five to eleven years.

Permanent control along these lines is only assured if resistance is effective over the whole range of possible variation in the pathogenicity of the pest. None of the varieties of potato at present undergoing registration trials in several countries, notably Britain, Germany and Holland, possess resistance of this ideal type.

There remains the possibility of alternating crops of potatoes possessing different kinds of resistance, effective against different strains of potato root eelworm, and achieving control by means of controlled population dynamics. Separate infestations can be treated as separate problems because any exchange of cysts between the more or less isolated populations infesting separate fields depends upon transportation of infested soil, against which precautions can be taken. The type of control envisaged must depend on the scope of resistance in relation to strain and must be based ultimately on the relationship between genes controlling resistance in potatoes and genes controlling

pathogenicity in potato root eelworm. This is the host/parasite relationship in the broadest sense.

Almost nothing is known of the biochemistry of resistance: the problem as a whole is outwith the scope of this thesis, which deals mainly with measurement of resistance. This is a matter of assessing the incidence of cysts on root systems after exposure to a known population of eggs or larvae. The relevant stages in the life history of the pest are illustrated. (Frontispiece). A fuller account of the life history is given as an Appendix.

SECTION I.

Variation in Pathogenicity of the Potato Root Eelworm (*Heterodera rostochiensis* Woll.,) and its Significance in Potato Breeding

1. INTRODUCTION

A prospect of breeding commercial varieties of potato with resistance to potato root eelworm, *Heterodera rostochiensis* Woll., originated with the finding of such resistance in four clones of *Solanum tuberosum* subsp. *andigena* (Juz. et Buk.) Hawkes in 1951 (Ellenby, 1952). Toxopeus and Huijsman (1952) showed that the resistance was hereditary and postulated (1953) that a dominant gene, designated H, conferred resistance in seedlings descended from the clone C.P.C.1673. Most of their resistant seedlings had cyst-free roots under conditions such that any susceptible segregates and the commercial varieties of potato used as susceptible controls had roots crowded with cysts. Jones (1954) established that the resistant root systems were invaded by potato root eelworm and that subsequently most of the larvae ceased to develop at various stages prior to sexual maturity. A few males matured in his material but adult females were virtually absent.

Potato breeding for resistance to eelworm was undertaken by the Plant Breeding Stations at Cambridge and at Pentlandfield, near Edinburgh, in 1952. The initial results obtained at both places agreed with the early findings of Toxopeus and Huijsman in the Netherlands. Evidently, the three sets of results were obtained with geographically

isolated populations of potato root eelworm of similar pathogenicity.

The first indication that populations could differ in pathogenicity towards plants of genotype H was noted at Pentlandfield in 1955 (Anon., 1956). In this instance, certain progenies in which the gene H was expected to occur were infected by a population from a garden in Edinburgh but none of the seedlings remained cyst-free. Investigations relating to this population, hereafter termed the Duddingston population, are reported in the following pages.

2. PATHOGENICITY OF THE DUDDINGSTON POPULATION OF HETERODERA ROSTOCHIENSIS

One hundred and seventy-eight cysts were picked from the roots of seven plants of genotype H growing in soil infested with the Duddingston population. The mean dimensions of these cysts, measured by projecting an image x 100 on centimetre graph paper, were 0.54 mm. in length from base of neck by 0.48 mm. in breadth, giving a length/breadth ratio of 1.12. These "Duddingston cysts" agreed with Heterodera rostochiensis Woll., in size, roundness, passage through the same colour changes and in possession of a single fenestra and the V-shaped mark. Henceforward, the Duddingston population was regarded as aggressive* Heterodera rostochiensis.

*The term "aggressive" denotes an increase in the facility with which a parasite overcomes resistance, and reproduces in the host. From Gäumann, Principles of Plant Infection. London. 1950.

This aggressiveness did not preclude the possibility that some residual resistance to the Duddingston population might be found in certain seedlings of genotype H. Such resistance, especially if present in seedlings already selected for their promising economic type, could be useful in breeding. It was also important to know if any such resistance in subsp. andigena had been dissipated in crosses with susceptible commercial varieties of potato. For these reasons, a comprehensive selection of material in the breeding line stemming from C.P.C.1673 was tested for resistance to the Duddingston population.

Possible alternative sources of resistance were explored in material descended from subsp. andigena C.P.C.1685 and C.P.C. 1690 and in S. vernei Bitt. et Wittm. A range of non-tuberous species of Solanum was also tested against the Duddingston population. It was established that British named varieties of S. tuberosum subsp. tuberosum, including many available from museum collections only, were susceptible to the Duddingston population.

Methods

It was desirable that the Duddingston population should be once "passed through" plants of genotype H to ensure as far as possible that the inoculum to be used in tests of resistance comprised solely the progenies of aggressive females. Accordingly, soil was obtained in which all the new cysts had arisen on a batch of plants at least simplex for the gene H. This soil was finely sieved to increase the number of cysts per gm. and to allow of its

admixture uniformly with sand of similar particle size. The infectivity of the sieved soil was 422 eggs per gm., prior to dilution with cyst-free sand and in a ratio calculated to give a culture medium containing 100 eggs per gm. The infectivity of the sandy culture medium proved to be 1.36 ± 0.07 cysts per gm. and 81.2 ± 2.1 eggs per cyst, or 110 eggs per gm.

Two plants of each clone under test were grown from tuber-pieces in 3-inch pots containing cyst-free sand until the shoots were a few inches tall, when the plants were tipped out of the pots. The intact root-balls were positioned centrally on a layer of the infested culture medium in the bottoms of 4-inch pots. The space between each root-ball and the walls of a pot was filled with more of the infested culture medium, until in all 200 gms. of it had been added to each 4-inch pot. The pots were sunk to the rims in a sand plunge (Plate 1), where an average temperature of 64°F was maintained by soil-warming electric cables connected to a thermostat.

The advantages of the method were held to be:

a. economical use of the infested culture medium,

b. infection was delayed until the plants were established and growing vigorously,

c. the cysts were concentrated in the zone where most root growth would take place.

Factors (b) and (c) were expected to contribute towards the rapid and uniform infection of the roots which would be exposed later when the root-balls were tipped out of the 4-inch pots. The incidence of cysts developing on these roots was recorded by the following method.

Plate 1. The sand plunge, showing soil-warming cables, thermostat cover, and empty pots in position.

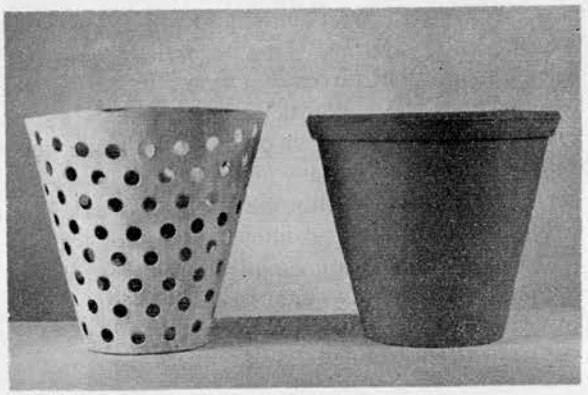


Plate 2. The "perforated can".

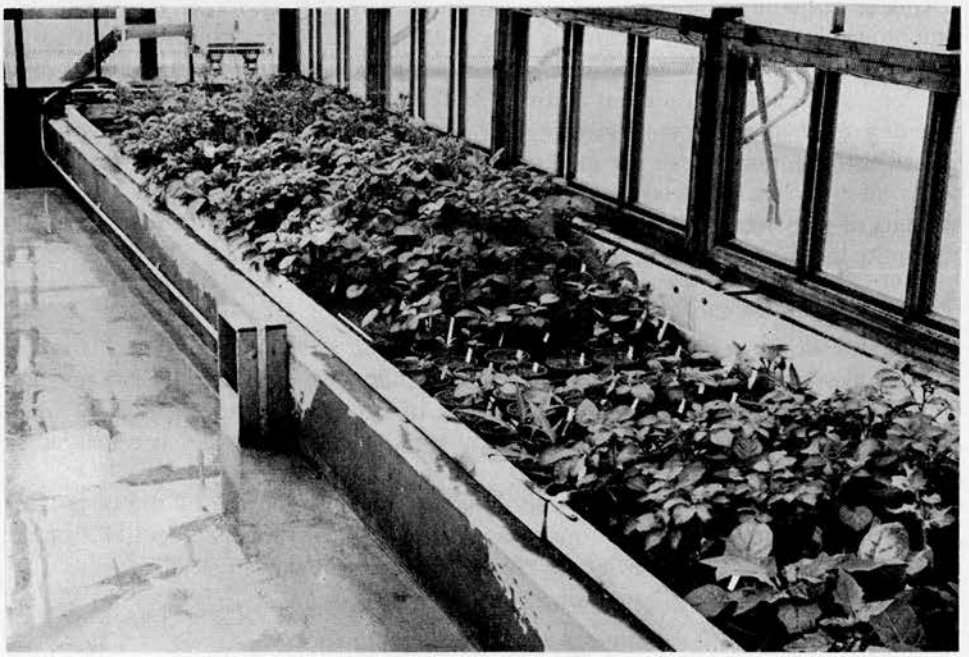


Plate 3. A range of material under test in the sand plunge.

Plate 4. Senescent plants of S. tuberosum subsp. tuberosum on left, with plants of subsp. andigena in full flower at right. The subsp. andigena comprises short-day plants which often fail to form tubers before being cut down by frost in Britain.

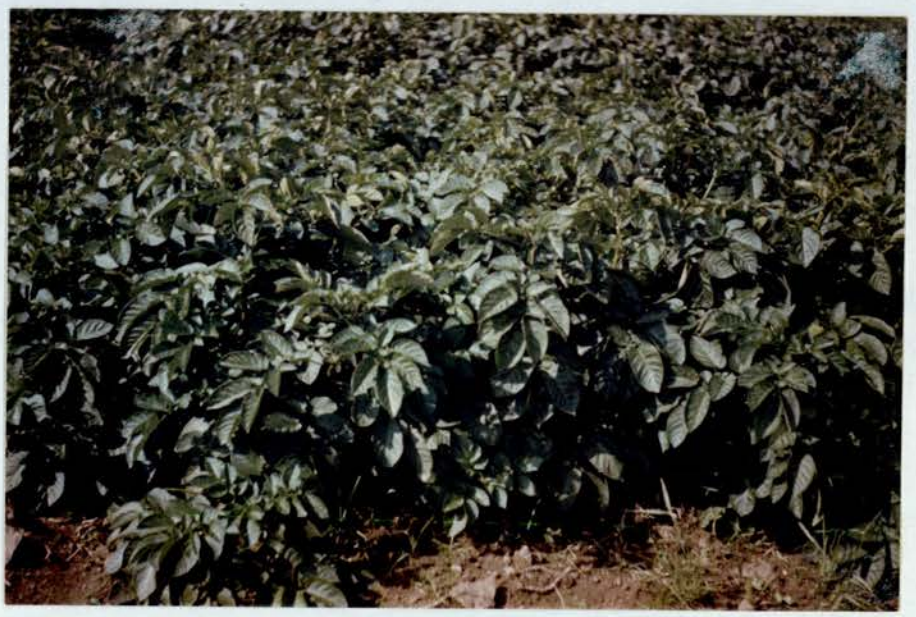


Plate 5. Clone incorporating the resistance of subsp. andigena. One of several undergoing final selection prior to entry into official registration trials.

Plate 6. Top left and bottom right: plots in which the susceptible, commercial variety Craigs Royal is growing for the second year in succession. The plants are stunted and dying, due to severe eelworm attack.

Bottom left and top right: Craigs Royal in plots where the infestation decreased during the previous year, due to the "trap cropping" effect of resistant potatoes bred from subsp. andigena C.P.C. 1673.

A "perforated can", made from thin copper sheeting, was used (Plate 2). This was a bottomless model of a 4-inch pot with 130 regularly spaced, circular holes or windows of 1/4 inch diameter in the wall. Together, these windows exposed to view about 16 per cent. of the surface of a 4-inch root-ball fitted into the can.

Counts were made of (a) the number of windows in which roots appeared, (b) the number of windows in which developing cysts were observed. Further experience showed that (c) the total number of cysts visible in all windows could also be counted without much extra trouble. The counts were facilitated by standing the perforated can on a turntable. These data enabled a "cyst index" to be calculated for each plant.

Test of material derived from C.P.C.1673

The material comprised 13 clones subsp. andigena, 15 clones from the cross between subsp. andigena and subsp. tuberosum and 16 clones from the first backcross to subsp. tuberosum, all incorporating the gene H. Cysts appeared on every plant and the clones were grouped according to the average cyst index of the two plants which represented each of them.

$$\text{cyst index} = \frac{\text{No. of windows showing at least one cyst}}{\text{No. of windows showing roots}} \times 100$$

It was apparent from the distribution of the cyst index as recorded in Table 1 that there was no appreciable difference in susceptibility between the generations of subsp. andigena selfed, crossed with subsp. tuberosum or

Material descended from subsp. *andigena* C.P.C.1673	Cyst index groups						
	I 0-5	II 5-10	III 10-15	IV 15-20	V 20-25	VI 25-30	VII 30-35
13 clones subsp. *andigena*.....	2	5	5	1	-	-	-
15 clones subsp. *andigena* x subsp. *tuberosum*.....	1	4	3	5	2	-	-
16 clones first backcross to subsp. *tuberosum*.....	1	5	5	3	-	1	1
Total clones.....	4	14	13	9	2	1	1

TABLE 1. CLASSIFICATION OF CLONES DESCENDED FROM C.P.C.1673 AND INFECTED BY THE DUDDINGSTON POPULATION.

Cyst index groups		I	II	III	IV	V	VI	VII
Average sieved soil per pot in gms.....	= a	688	684	678	675	691	674	688
Average number of cysts per 100 gms sieved soil	= b	142	201	242	266	384	352	491
Average number of eggs or larvae per cyst.....	= c	122	104	-	-	-	-	-
		Estimated initial cysts per pot.... = d 272 Estimated initial egg population... = e 22,086						
Yield of cysts per pot $\frac{a \times b}{100}$	= f	977	1,375	1,641	1,795	2,653	2,372	3,378
Multiplication in terms of cysts.....	= f/d	3.6	5.1	6.0	6.6	9.8	8.7	12.4
Yield of eggs per pot.....	= f x c	119,194	143,000	-	-	-	-	-
Multiplication in terms of eggs.....	= $\frac{f \times c}{e}$	5.4	6.5	-	-	-	-	-

TABLE 2. RECOVERY OF THE PARASITE FROM GROUPS OF CLONES AS CLASSIFIED IN TABLE 1.

backcrossed to subsp. tuberosum. There remained the possibility that any clone, irrespective of generation, possessed a useful level of resistance if classed in a group with a low cyst index. Therefore, the next step was to determine the extent to which the initial population of eelworm had declined or multiplied in association with the clones as grouped in Table 1.

The culture medium in which each group had grown was sieved and weighed. Then cysts were recovered by flotation from nine samples of 100 gms. taken from the bulks of culture medium corresponding to each group. Samples of cysts were collected from the calculated quantities of culture medium required for a yield of 100 cysts and the mean egg content of three such samples from each bulk of culture medium was estimated by Goodey's method (1951). No attempt was made to distinguish between new cysts and cysts of an older generation.

In the second part of Table 2 the yield of cysts and eggs from the different groups is calculated per pot and is expressed as a multiple of the inoculum in terms of cysts and in terms of eggs. Infectivity (eggs per gm.) in the culture medium from the two least susceptible groups proved to be 5.4 and 6.5 times greater than the initial infectivity. This rate of multiplication on the least susceptible clones did not appear to warrant their use as sources of resistance in a breeding programme. It was concluded that no useful resistance to the Duddingston population was present in the breeding line stemming from C.P.C.1673.

The validity of the grouping by cyst index was supported

by the data in Table 2 showing the number of cysts recovered from the different groups at the end of the growing period. The perforated can method appeared to be a reliable and objective method of assessing the incidence of cysts on a root system, less laborious than the recovery of cysts by flotation, with the added advantage that the calculation of cyst index compensated to some extent for variations in mass of root system produced by different clones.

Test of material descended from subsp. andigena C.P.C.1685 and C.P.C.1690

Certain clones bred from subsp. andigena C.P.C.1685 and C.P.C.1690 were tested for resistance to the Duddingston population. These clones, selected because of their freedom or near freedom from cysts in previous tests of resistance to potato root eelworm, are listed below against cyst indices obtained with the Duddingston population.

Descended from C.P.C.1685:-	Cyst indices
1 clone subsp. andigena selfed	10.3
3 clones subsp. andigena x subsp. tuberosum	12.0, 27.7, 46.8
Descended from C.P.C.1690:-	
2 clones subsp. andigena selfed	17.2, 19.1
2 clones subsp. andigena x subsp. tuberosum	15.7, 20.4

A comparison of the cyst indices with those recorded in Table 1 for material bred from C.P.C.1673, was sufficient to indicate that C.P.C.1685 and C.P.C.1690 possessed no resistance to the Duddingston population that could be useful in breeding.

Test of Solanum vernei

Ellenby (1948) reported that S. vernei was resistant

to potato root eelworm. S. vernei is diploid and indigenous to Argentina; no cultivated varieties of it are known. Six clones of the species were obtained in 1956 from Dr K. S. Dodds of the John Innes Horticultural Institute.

One plant of each clone was tested for resistance to the Duddingston population and a second plant of the same clone was tested against a non-aggressive population, namely the Boghall population, of comparable infectivity (105 larvae per gm.) achieved by diluting sieved, infested soil with cyst-free sand. All the plants remained cyst-free excepting one which was seen to support one small cyst after exposure to infection by the Boghall population. Therefore, S. vernei retained its resistance against the Duddingston population and differed in this respect from the clones C.P.C.1673, C.P.C.1685 and C.P.C.1690 of subsp. andigena.

Test of non-tuberous Solanaceae

A range of species other than potatoes in the family Solanaceae and Antirrhinum majus L. (Scrophulariaceae) were tested against the Duddingston and Boghall populations. Four plants of Solanum nigrum L. and two plants of the other species were tested against each population. The objective was to determine whether or not aggressiveness as manifest towards the clone C.P.C.1673 of subsp. andigena had led to confusion in the records of host susceptibility as summarised, for instance, by Franklin (1951). It was also of interest to know whether or not plants of the species indigenous to Britain were differential hosts for the

Species	Cysts per 100 windows showing roots	
	Boghall population	Duddingston population
S. aviculare	39.3, 43.2	16.9, 38.7
S. dulcamara	1.7, 6.0	2.4, 0
L. esculentum	0 , 2.5	0.8, 0.8
S. nigrum seed stock 1 ...	0 , 0	1.6, 2.3
S. nigrum seed stock 2 ...	0 , 0	2.4, 2.3

TABLE 3. CYST INDICES OF PAIRS OF PLANTS.

Duddingston and Boghall populations. In this respect the position of S. nigrum was important. Here a degree of resistance apparently comparable to that found in subsp. andigena was well authenticated (Doncaster, 1953). S.nigrum is a common weed of arable fields in some parts of Britain.

A. majus was represented in the test because Franklin (1951) recorded "cysts that were probably H. rostochiensis" on a plant or plants of this species. Therefore, the prevalence of A. majus in gardens and the garden origin of the Duddingston population were possibly related facts.

The plants of the following species remained free from cysts throughout the test:-

Antirrhinum majus L., Atropa belladonna L.,
Datura stramonium L., D. inermis Jacq.,
Hyoscyamus aureus All., Lycium chinense Mill.,
Nicotiana alata Link et Otto, N. rustica L., N. tabacum L.,,
Physalis alkekengi L., Solanum capsicastrum Link.

Cysts developed on roots of the plants of the following species after infection by one or both populations:-

Solanum aviculare Forst., S. dulcamara L.,
S. nigrum L., Lycopersicum esculentum Mill.
var. Moneymaker.

The incidence of cysts on these plants was recorded by use of the perforated can. On this occasion cysts were counted and the cyst index for each plant is given in Table 3 as number of cysts per hundred windows showing roots.

The plants of S. aviculare, a species limited in distribution to Australasia, where potato root eelworm is not reported to occur, were very "good" hosts for both populations. The plants of the remaining species were "poor" hosts by comparison with S. aviculare. Neither population appeared to be well adapted for multiplication

in L. esculentum nor in S. dulcamara. A few cysts were observed on each of four plants of S. nigrum infected by the Duddingston population, while the plants exposed to infection by the Boghall population remained cyst-free. Reference to the literature suggested that cyst formation in S. nigrum was noteworthy. For instance, Doncaster (1953) catalogued the development of larvae in roots of S. nigrum and showed that development ceased before cyst formation. Jones (1950) studied the host ranges of several Heterodera sps., including potato root eelworm, but recorded no cysts on S. nigrum. It was concluded that the Duddingston population was aggressive towards S. nigrum. The possibility of a significant parallel between this relationship and the aggressiveness of the Duddingston population towards potatoes having the resistance of subsp. andigena C.P.C.1673 is a subject for more general discussion (page 29).

Test of British named varieties of potato

Stocks of the following varieties were obtained from the Department of Agriculture and Fisheries for Scotland, through the courtesy of Dr J. Hardy, East Craigs Seed Testing Station, Edinburgh:-

1. Ally
2. Angus Leader
3. Arran Banner
4. Arran Bard
5. Arran Chief
6. Arran Comrade
7. Arran Crest
8. Arran Luxury
9. Arran Pilot
10. Arran Rose

11. Ballydoon
12. Beauty of Bute
13. Bishop
14. British Queen
15. Catriona
16. Champion
17. Di Vernon
18. Doon Early
19. Dr McIntosh
20. Dunbar Cavalier
21. Early Market
22. Eclipse
23. Edzell Blue
24. Epicure
25. Gladstone
26. Golden Wonder
27. Great Scot
28. Harbinger
29. Herald
30. Herd Laddie
31. Hibernian
32. Irish Queen
33. John Bull
34. Katie Glover
35. Kerr's Pink
36. King Edward
37. King George
38. Lord Rosebery
39. Lymm Gray
40. Magnum Bonum
41. Magnificent
42. Majestic
43. Marquis of Bute
44. May Queen
45. Ninetyfold
46. Northern Star
47. Old Black
48. President
49. Pride of Bute
50. Puritan
51. Reading Russet
52. Record
53. Redskin
54. Rocks
55. Royal Kidney
56. Shamrock
57. Sharp's Pink Seedling
58. Shetland Black
59. Stirling Castle
60. Summit
61. Sutton's Abundance
62. Sutton's Early Regent
63. Tinwald Perfection
64. Ulster Chieftain
65. Up-to-Date
66. Witchhill
67. Yam

Two plants of each variety were tested against each of the Duddingston and Boghall populations. Every plant was found to support abundant cysts. It was concluded that a useful level of resistance to the Duddingston population in commercial varieties of potato could only be achieved by breeding, starting with resistant species of potato such as S. vernei.

3. THE DISTRIBUTION OF AGGRESSIVE POPULATIONS OF HETERODERA ROSTOCHIENSIS

The populations of potato root eelworm infesting 113 fields or gardens were tested for pathogenicity towards potato plants having the resistance conferred by the gene H originally present in subsp. andigena C.P.C.1673.

The samples of infested soil from these fields and gardens were grouped as follows:-

a. 15 samples from gardens in the Duddingston area of Edinburgh, and from fields near Edinburgh,

b. 8 samples from fields in West Ayrshire that had been cropped annually with Epicure, a "first early" variety of potato reputed to possess some resistance to potato root eelworm,

c. 5 samples from fields in East Anglia,

d. 85 samples from fields in fifteen Scottish counties.

The samples were finely sieved and two infested potting soils were prepared from each to give two series of soils (Series I and II) of similar physical structure and fertility but of relative infectivity 1:3. No attempt was made to standardise infectivity within a Series.

Series I. -

1 part sieved soil : 3 parts cyst-free soil supplement by volume.
(Soil supplement = 1 peat : 11 compost, $\frac{2}{3}$ oz. potato fertiliser per gall.).

Group	Sample No.	Cyst index			
		Pentland Ace		Clone of genotype H	
		SERIES I	SERIES II	SERIES I	SERIES II
a	1	12.9	12.2	30.1	13.7
	2	10.5	9.0	10.3	19.8
	3	4.8	12.0	10.3	21.3
	4	19.3	42.7	2.0	1.0
	5	36.6	21.7	2.0	3.0
	6	53.6	34.7	2.8	7.6
c	7	50.0	31.1	44.7	32.6
d	8	1.0	0	5.5	4.1
	9	3.0	damaged	3.3	2.2
	10	2.5	3.1	0.9	4.3
	11	6.4	11.9	11.6	15.5
	12	2.8	11.8	1.0	14.5
Non-aggressive control		92.2	44.7	0	0

TABLE 4. LIST OF SOIL SAMPLES CONTAINING AGGRESSIVE POPULATIONS AND CYST INDICES WITH PENTLAND ACE AND A CLONE OF GENOTYPE H.

Series II. -

3 parts sieved soil: 1 part cyst-free supplement by volume.
(Soil supplement = 3 peat : 1 compost, 2 ozs. potato fertiliser per gall.).

Each of the original samples was finally represented by a pair of full 4-inch pots in both Series I and Series II. Pentland Ace was grown as the susceptible control variety of potato in one pot of each pair. A seedling variety of genotype H was grown in the other pot of each pair. All the pots were sunk to the rims in an outdoor gravel plunge.

Root-balls were inspected when yellowing cysts were visible on the controls. A population was classed as "aggressive" when cysts were found to be developing at the same time on the plants of genotype H.

Few or no cysts appeared on the susceptible controls growing in the Series II soils prepared from 15 of the original soil samples. These samples were excluded from further consideration because the level of infectivity in them must have been very low.

Twelve of the remaining 98 samples contained aggressive populations and are listed in Table 4 with cyst indices obtained by using the perforated can. These data reflected expected differences in the level of infectivity within series and there was a definite relationship between the incidence of cysts on Pentland Ace in Series I and II, viz., when the cyst index in Series I was low it was almost invariably higher in Series II (samples Nos. 3, 4, 11 and 12) and vice versa (samples Nos.6, 7 and the non-aggressive control). In the latter cases it seemed probable that

root decay and severe competition between developing larvae following excessive invasion of the root systems had depressed the yield of cysts in Series II, in which the soils were always three times more infective than the corresponding soils in Series I. The cyst indices for the seedling of genotype H showed the same trends, but only when a population appeared to be fully aggressive.

Nine of the aggressive populations were fully aggressive, giving very similar cyst indices with plants of Pentland Ace and plants of genotype H. The remaining three aggressive populations (Nos. 4, 5 and 6) were clearly less well adapted for multiplication on plants of genotype H.

Four of the aggressive populations occurred in the samples of soil from gardens in Edinburgh. Sample No.1 was from the garden where the Duddingston population had been obtained previously, and samples 2 and 3 came from adjacent gardens. Information obtained locally suggested that this was an area where dwelling houses had been built recently on farm land infested with potato root eelworm. Formerly, this land had been cropped at short intervals with the early-maturing variety of potato called Epicure. Since a degree of resistance to potato root eelworm was claimed for Epicure by Gemmel (1943) its cultivation was a factor that might help to explain the distribution of aggressive populations.

Accordingly, the eight samples in group (b) were collected in the Coastal region of Ayrshire from fields in which Epicure had been grown annually for many years. One

sample came from a field in which Epicure potatoes had been attacked annually by potato root eelworm since before 1930. This type of monoculture remains practicable if crops of immature tubers are harvested for the early market before the developing cysts of potato root eelworm contain a full complement of eggs. O'Brien and Prentice (1932) and Grainger (1951) discussed the cultivation of potatoes in this area.

None of the populations comprising group (b) proved to be aggressive. This finding tended to discount any causal relationship between the cultivation of Epicure and the distribution of populations aggressive towards potatoes of genotype H.

Eight of the aggressive populations were found in samples from widely separated fields in Southeast and Southwest Scotland and East Anglia. A study of the distribution of the aggressive populations failed to reveal any historical or environmental factors seemingly associated with the evolution of aggressive populations.

DISCUSSION

During the first two or three years of breeding for resistance to potato root eelworm there was evidence that biotypes of the pest occasionally survived to female maturity in potatoes incorporating a resistance gene H, present originally in the clone C.P.C.1673 of S.tuberosum subsp. andigena (Toxopeus and Huijsman, 1952; Jones, 1954). There was no evidence, however, that the probability of a potentially female biotype surviving in a plant of genotype H increased in the survivors' progenies. There remained the

possibility that the resistance of subsp. andigena C.P.C. 1673 was of the ideally useful type, proof against the whole range of possible variation in the pathogenicity of the pest.

This possibility must be dismissed in view of the multiplication of the Duddingston population on potatoes of genotype H. This type of aggressiveness was detected in 10 per cent. of the populations sampled in a preliminary survey of pathogenicity of potato root eelworm in Britain. There was no history of association between the aggressive populations and potatoes of genotype H since these were unavailable to commercial growers.

There is thus a problem of how to account for the extreme variation between populations in pathogenicity towards potatoes of genotype H. Some populations contained few or no aggressive biotypes and others so many that potatoes of genotype H were fully susceptible. Still others were intermediate in pathogenicity, either because they contained an intermediate proportion of fully aggressive biotypes or because all or most of the biotypes comprising them had an intermediate chance of survival in a plant of genotype H.

To state that the gene H at no time conferred resistance to all populations of potato root eelworm in Britain merely raises the same problem.

The present distribution of aggressive populations may be wholly a matter of chance, if it is accepted that the difference in pathogenicity arose by mutation in Britain and was without effect on the survival and multiplication

of potato root eelworm until the introduction of potatoes of genotype H. Before this, the greater difference between populations would be due to the initiation of separate infestations by aggressive biotypes alone and by non-aggressive biotypes alone. Smaller differences might result from mutation in established infestations or from the contamination of such infestations with cysts of different origin.

The basic hypothesis above can be elaborated in the knowledge that potato root eelworm is indigenous both to Bolivia (Bell and Alandia, 1955), where the clone C.P.C.1673 was collected (Jones, 1954) and to the adjoining country of Peru (Bazán de Segura, 1952), where a population aggressive towards potatoes of genotype H was found (Quivedo Diaz et al, 1956). Therefore, selective multiplication of aggressive biotypes may have taken place in regions in South America where aggressiveness could be an important factor affecting survival. Subsequently, in the four centuries since the potato was first brought to Europe from South America, aggressive biotypes may have been introduced into Europe, where the aggressive character may have been perpetuated without expression until the bringing together of the Duddingston population and of potatoes of genotype H.

Another elaboration would be to postulate a factor or factors in Britain discriminating to some extent against the survival of biotypes either aggressive or non-aggressive towards potatoes of genotype H. The presence of S. nigrum as a weed in arable fields could be such a factor since the Duddingston population, typically aggressive towards plants

of genotype H, was also aggressive towards S. nigrum. In future, it may be possible to decide whether or not these two manifestations of aggressiveness are correlated or independent attributes of H. rostochiensis.

Whatever the theoretical outcome, the area of land infested in Britain where the resistance of subsp.andigena C.P.C.1673 could be used effectively is reduced by a first estimate of 10 per cent. The period of continued effectiveness of resistance in the remaining area will probably vary, since the populations infesting different fields may differ in long term response to the cultivation of resistant potatoes. Fortunately, since potato root eelworm is a soil-borne pest, the spread of aggressive biotypes depends mainly on the transportation of infested soil adhering to farm products and implements and can be minimised by appropriate precautions.

Meanwhile, it appears that the cultivation of potatoes possessing the resistance of subsp. andigena may contribute towards the control of potato root eelworm, without offering a complete solution to the problem. In future, it may be possible to widen the scope of control by utilising the resistance of S. vernei.

SECTION II.

Variation in Pathogenicity of the Potato Root Eelworm (*Heterodera rostochiensis* Woll.) : Techniques and Results of Testing Wild Potatoes for Resistance

In *Solanum tuberosum* subsp. *andigena*, particularly the clone C.P.C.1673, potato breeders had parental material possessing the advantage of near relationship to commercial varieties of potato combined with a very high level of resistance to potato root eelworm, due to a dominant gene designated H by Toxopeus and Huijsman (1953). Breeding progressed rapidly to the stage at which it could be said that no inherent obstacle existed to prevent the incorporation of this very high level of resistance in a new variety of potato. It was believed that cropping with such a variety would extend the "starving out period" between crops of susceptible potatoes and in addition, by stimulating the hatching of larvae which then failed to mature in the resistant plants (Jones, 1954), would augment the natural decline of infestation in the absence of susceptible potatoes.

These propositions are still valid, but of limited application because the *andigena* type of resistance does not prevent the multiplication of certain aggressive populations of potato root eelworm now known to occur in Britain (Dunnett, 1957; Jones, 1957) and also in Peru (Van der Laan and Huijsman, 1957). For practical purposes, these aggressive populations represent a specialised strain. The evolutionary process of specialisation has not,

however, been observed, since fully aggressive populations existed in Britain inadvance of the introduction of potatoes of genotype H. In surveys of the pathogenicity of potato root eelworm in Britain, 10 per cent. (Dunnett, 1957) and 70 per cent. (Jones, 1957, 1958) of the sample populations were classed as aggressive.

Consequently, there was initiated a search for parental material with a useful level of resistance to populations aggressive towards potatoes of genotype H. S. vernei, found to be equally resistant to the aggressive and non-aggressive populations (Dunnett, 1957; Jones, 1958) meets this requirement. The species is diploid but colchicine-induced tetraploid forms have been crossed with commercial varieties of S. tuberosum and further breeding is being done in Britain, Germany and the Netherlands. Nothing can be gained at present by attempting to forecast the outcome of this breeding. Instead, it is prudent to continue the search for resistance to aggressive populations, to replace or supplement the resistance of S. vernei if the need should arise. An account of this kind of work will be reported here. Results will be discussed in relation to the historical background of research into the host/parasite relationship.

MATERIAL AND METHODS

Three collections of wild potatoes were tested for resistance. These were,

(1) 327 clones, unidentified as to species, part of a South American collection made by Dr H. Toxopeus of the Netherlands (Toxopeus, 1956);

(2) 55 samples of seed of various species or from crosses between species, supplied by Dr J.G.Hawkes of Birmingham University;

(3) a group of selected clones, comprising 10 clones of S. vernei, 2 clones of S. famatinae, 5 unidentified clones of triploid constitution, 5 clones of S. demissum and 2 control clones, namely, 71/1 and 71/17, originally resistant and susceptible segregates from the same progeny in the breeding line stemming from subsp. andigena C.P.C. 1673. The clone 71/1 incorporated with gene H and 71/17 was for use as the susceptible control.

Dr H.Ross of the Max-Planck Institut, Cologne, supplied the clones of S. famatinae and five of the clones of S. vernei.

The first two groups of material were screened for resistance to the Duddingston population, aggressive towards potatoes of genotype H. The third group was tested additionally aginst the Boghall population, non-aggressive towards potatoes of genotype H.

The tests were conducted as described on pages 7-13 except in two respects. Firstly, tubers were planted in 4-inch pots containing culture medium of 40 eggs/gm. infectivity, instead of starting the plants in 3-inch pots containing cyst-free sand prior to surrounding the root-balls, when transferred to 4-inch pots, with culture medium of 100 eggs/gm. infectivity. Secondly, plants raised from seed were pricked into 3-inch pots for the duration of the tests, since it was uncertain that they would become sufficiently pot-bound in larger pots.

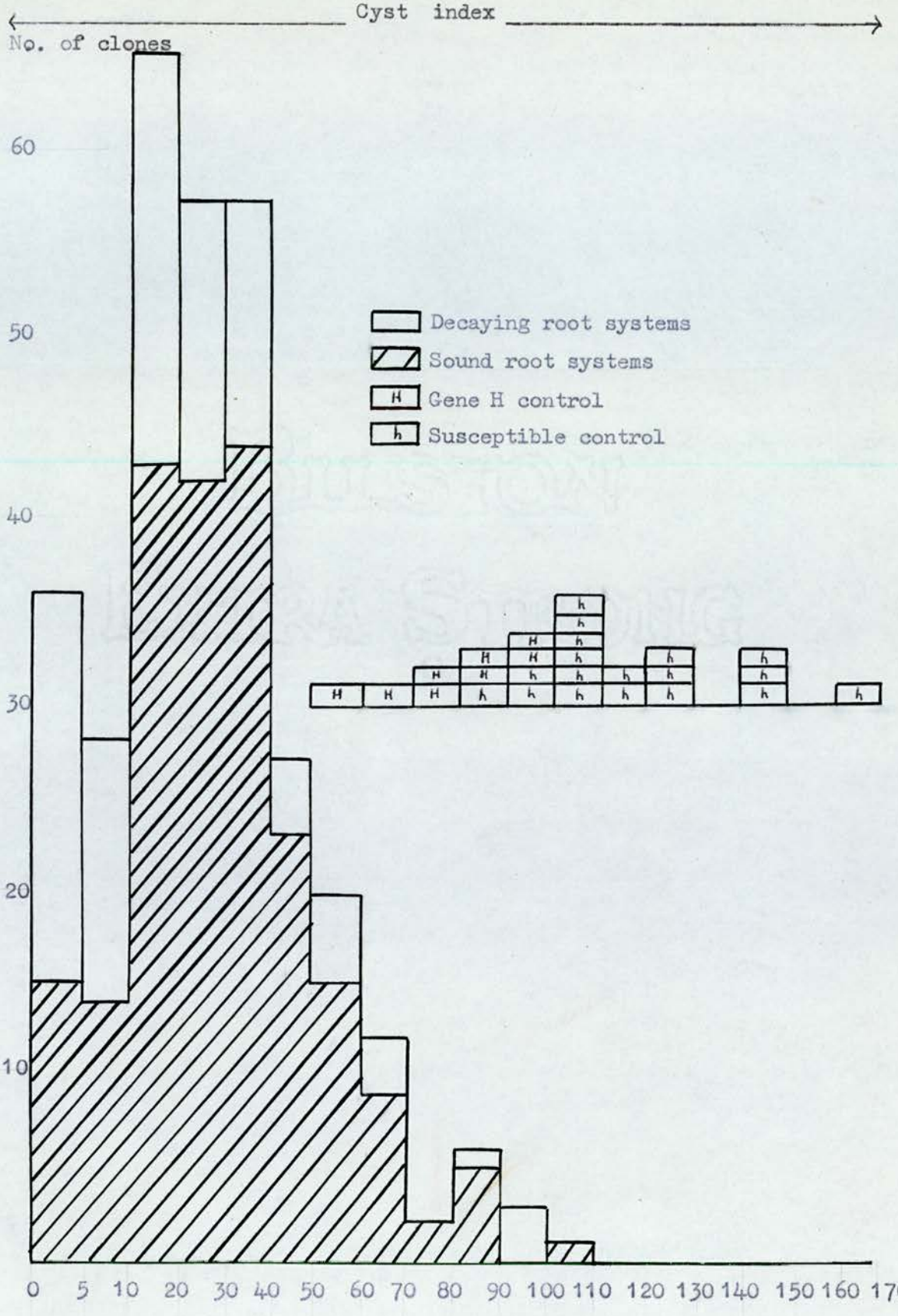
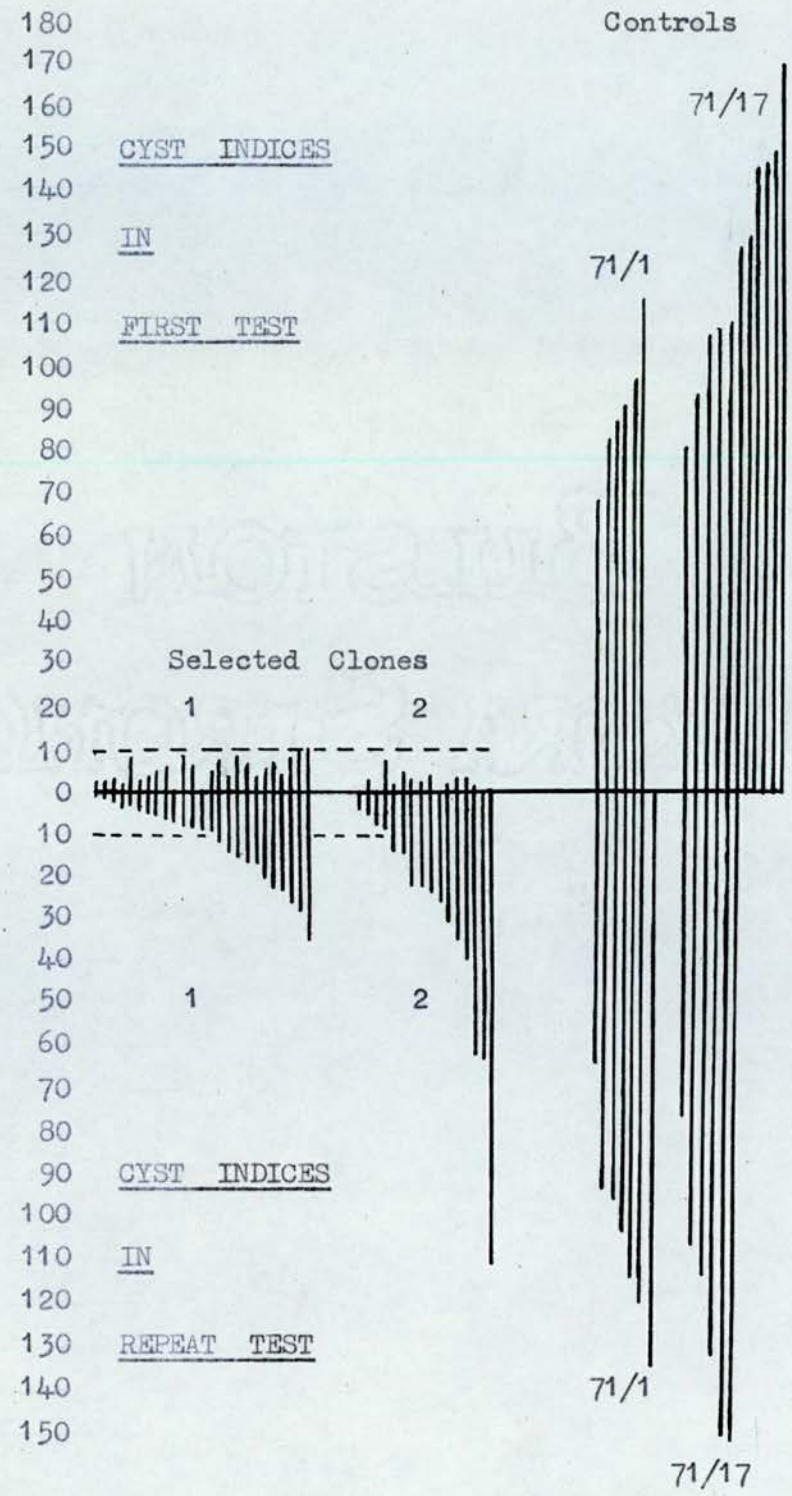


FIG. 1. DISTRIBUTION OF 327 CLONES ACCORDING TO CYST INDEX OBTAINED WITH THE DUDDINGSTON POPULATION.



RESISTANCE TO THE DUDDINGSTON POPULATION IN SELECTED CLONES.

FIG. 2.

RESULTS

(1) The screening of 327 clones of South American origin for resistance to Duddingston eelworm population

Fig.1 illustrates the distribution of the clones according to stated intervals in the range of a cyst index ascribed to them as a result of scoring a single plant clone by means of the perforated can. The unshaded parts of the histogram represent plants which had partially decayed root systems, giving poor conditions for cyst formation.

None of the clones remained free from cysts but very few were as susceptible as either 71/1 or 71/17, which had cyst indices about four times greater than the mean cyst index of the 327 clones under test. All clones having a cyst index of five or less were selected for a repeat test of resistance, as were clones with a cyst index less than ten, provided there was no record of root decay.

The cyst indices for a plant of each clone in the first and repeat tests are indicated by points above and below the base line, respectively, in Fig.2. The two points for each clone are connected by a straight line. The clones are arranged in order of increasing cyst index in the repeat test, and a separate grouping is reserved for clones which had partially decayed root systems in the first test. The estimates of cyst index for 71/1 and 71/17 are also arranged in ascending order.

Clones that had decaying root systems and a low but suspect cyst index in the first test tended to behave in the same way in the repeat test, when 50 per cent. of them (12 plants) again had decaying root systems. Of the plants

which had sound root systems in the first test, only one out of 25 plants showed signs of root decay in the repeat test. These facts are mentioned because the root systems of some clones may be inherently intolerant of invasion by larvae, a defence mechanism which could result in the starvation of larvae thus isolated in dead and decaying rootlets. This is sometimes referred to as "root pruning". But any factor leading to weakened growth may be an indirect cause of root decay, in that the weaker plants in a batch are often overwatered and may be waterlogged.

Any unsuitability of conditions for cyst formation was a factor almost certain to influence the selection of plants on a "few cysts" basis, even where the root systems were apparently sound (Group 1) and, in the case of plants which were recorded as having decaying root systems in the first test (Group 2), could conceal considerable susceptibility. In fact, for Groups 1 and 2 respectively, the mean cyst index in the repeat test was greater by 2.4 and 8.6 times. In Group 1, almost exactly half of the clones now fell outside the original limit for selection, but the discontinuity between the selected clones and 71/17, the susceptible control clone, largely remained. The high cyst indices recorded for 71/1, the clone of genotype H, was a reminder of the aggressiveness of the Duddingston population.

The majority of clones falling within the original limit of selection in the repeat test conformed to the same morphological type, although genotypic differences could be deduced from the shape and colour of the tubers. These plants had little or no stainable pollen and set no seed

Serial No.	Provisional identification	Number of Cysts								Mean cysts
		0	1-2	3-5	6-11	12-24	25-49	50-99	100-200+	
1	S. vernei subsp. ballsii	++++++								0
2	S. acaule x S. sanctae-rosae	+++++								0
3	S. sanctae-rosae	++++	+							0.6
4	Unidentified		+							1.0
5	S. vernei subsp. ballsii x S. simplicifolium	+++	++							1.0
6	Unidentified x Unidentified	++++	+		+					1.3
7	S. megistacrolobum	+++	+	+						1.5
8	S. neo-hawkesii	+	+++	+						1.7
9	S. multidissectum	++++			+					1.8
10	S. canasense	++++			+					2.0
11	S. vernei subsp. ballsii x S. simplicifolium	+++		++						2.2
12	Unidentified	+	++	+	+					2.3
13	S. simplicifolium	+	+++		+					2.5
14	Unidentified		++	+	++					3.7
15	S. chacoense	++			+					4.0
16	S. megistacrolobum	++				+				4.3
17	S. chacoense	+	++		+	+				4.8
18	S. demissum	+++	+++++	++++++++	+++++++++	+++				6.0
19	S. acaule subsp. aemulans		+		++++					6.5
20	S. megistacrolobum				++	+				7.5
21	S. gourlayi				+++	++				8.7
22	S. vernei x S. leptophyes		++				+			8.7
23	Unidentified x S. leptophyes				++++	++				10.3
24	S. vernei x S. simplicifolium			+	+	+++				10.7
25	S. vernei subsp. ballsii x S. simplicifolium		+		++	+++				10.8
26	S. acaule		+		++	+++				11.3
27	S. nigrum				+++	+++				11.3
28	S. chacoense		+++		+		++			15.8
29	Unidentified x S. chacoense				++	++	+			17.2
30	S. tarijense				+++		+++			18.2
31	S. chacoense x S. vernei subsp. ballsii	+			++	+	+	+		18.7
32	S. acaule subsp. aemulans				+	++	+++			21.6
33	S. chacoense				+		++			22.3
34	S. acaule					++++	+			23.0
35	S. raphanifolium	+				+	+	+		25.8
36	S. chacoense		+			++	+		+	36.0
37	S. tarijense nat. hybrid				+		+	++		37.5
38	S. chacoense x S. simplicifolium					+++	+	+	+	39.7
39	S. chacoense				+		+++	++		40.0
40	Unidentified x S. chacoense					++	++	+	+	42.0
41	S. tarijense nat. hybrid						+++	+++		42.5
42	S. chacoense					+		+		47.5
43	S. simplicifolium x S. leptophyes					+	++	++	+	49.2
44	S. chacoense							++	+	66.7
45	Unidentified					+				71.7
46	Unidentified							+	+	82.0
47	S. chacoense x S. leptophyes						++		+++	96.7
48	? S. chacoense							+	++++	120.0
49	S. chacoense								++++++	183.3
50	71/1 control, resistance gene H.								+++++++	200+
51	71/17 control, gene H absent								+++++++	200+

FIG. 3. DISTRIBUTION OF SEEDLINGS ACCORDING TO NUMBER CYSTS EXPOSED OVER 3 INCH ROOT-BALLS: DUDDINGSTON POPULATION.

after cross pollinations. Cytological examination revealed their triploid constitution and they were provisionally identified as Solanum juzepczukii Buk. by Dr H. Howard of the Cambridge Plant Breeding Station. The triploid clones were retained for experimental purposes and are discussed again under section 3 of the results (page 47).

(2) The screening of seedling progenies of wild potatoes for resistance to the Duddingston population.

In addition, a progeny of S. nigrum, the woody nightshade, was tested for resistance. When available, usually six seedlings from each progeny were transplanted into 3-inch pots of the Duddingston culture medium. Six seedlings were grown in order to give a reasonable chance of detecting at least one resistant segregate in any progeny comprising resistant and susceptible segregates. Six plants of each of the clones 71/1 and 71/17 were grown from tuber-pieces.

Fig.3 illustrates the results of counting the total number of cysts developing over the surfaces of the root-balls from 3-inch pots. Each symbol represents a seedling falling within one of several arbitrary subdivisions in the range 0-200 cysts. The subdivisions are arranged so that each interval is approximately twice the preceding one. This arrangement reflects the greater accuracy possible in counting cysts if few were present and attempts a critical classification of the potentially more useful seedlings, those bearing fewest cysts. When the progenies were listed in order of increasing mean number of cysts, the scatter was as shown in the diagram.

Maximum susceptibility in this test was displayed by 71/1 and 71/17, all plants of which were seen to support more than 20^0 cysts, irrespective of the gene H present in 71/1. At the other end of the scale, no cysts were seen on the six plants of S. vernei. Given these extremes of susceptibility and resistance, it was necessary to fix an intermediate point beyond which the more susceptible progenies, although having some mean resistance relative to the susceptible control clone, were unlikely to be useful sources of resistance in breeding work, unless resistant segregates were clearly present. With this requirement in mind, the list was divided at position 18 in the list, at the level of a mean count of six cysts.

Interspecific crosses with S. vernei occupied positions 5, 11, 22, 24 and 25, in order of increasing mean cyst count. No cysts were observed on 27 per cent. of these hybrids, and the data appeared to support the interpretation of a continuous range of resistance in hybrids with S.vernei, as distinct from a segregation of resistant and susceptible types.

A single cyst was detected on one of five plants of S. sanctae-rosae (position 3) and the remainder were cyst-free. In addition, all five seedlings of the cross S. acaule x S. sanctae-rosae (position 2) remained cyst-free. Since S. acaule (positions 19, 26, 32, 34) appeared to be fairly susceptible to the Duddingston population, it was concluded that S. sanctae-rosae compared very favourably with S. vernei as a source of resistance to the Duddingston population.

More than half of the seedlings were cyst-free in two out of three progenies of S. megistacrolobum (positions 7 and 20), a species close to S. sanctae-rosae taxonomically.

One cyst-free segregate occurred in a progeny of S. raphanifolium (position 35), again included in the same taxonomic series as the two preceding species (Megistacroloba Card. et Hawkes). It will be necessary to confirm the segregation, however, since the evidence for it depends at present on the classification of a single plant.

Cyst-free plants occurred in the progenies of S. neohawkesii, S. multidissectum and S. canasense (positions 8, 9, 10) and the incidence of cysts on the remaining plants in these progenies was never high. These are three species in the series Tuberosa. The plants of S. canasense were weak and poorly rooted.

The progenies of S. simplicifolium and S. demissum (positions 13, 18) were notable for low incidence of cysts, although cyst-free plants were now in the minority. S. demissum is a hexaploid species which yields tetraploid hybrids in crosses with diploid species such as S. vernei. The hybrids can then be crossed with commercial varieties of S. tuberosum, all of which are tetraploid, in order to establish breeding lines utilising the resistance of the diploid species. A further investigation into the resistance of S. demissum is reported in pages 47-51.

The intermediate position of S. nigrum in the list is significant because plants from the same seed stock remained free from cysts of the non-aggressive Boghall eelworm population in a previous test. In that test, too, cysts of the Duddingston population arose on S. nigrum (page 21).

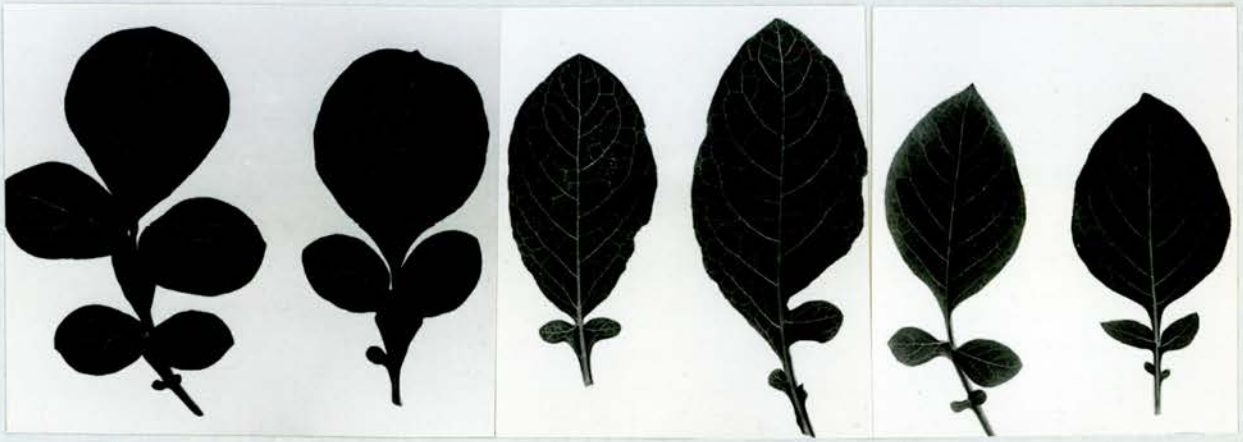
(a)

(b)

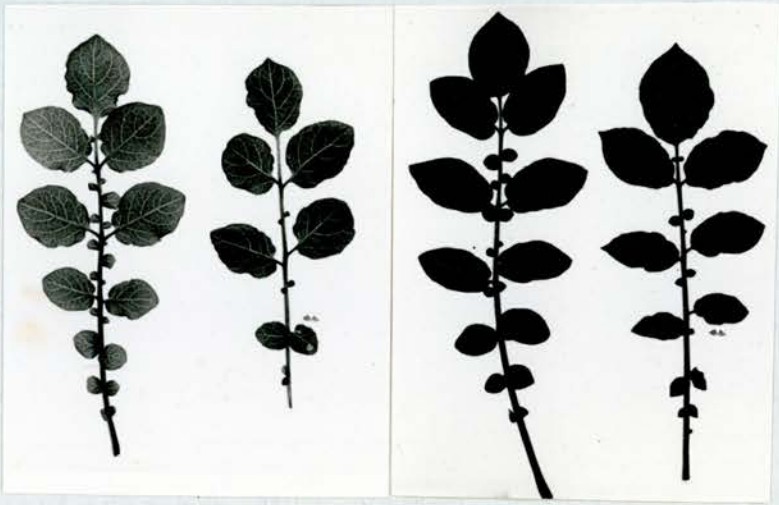
Plate 7. Species of potato resistant to root eelworm.

(a) Series Megistacroloba
Front row : S. sanctae-rosae.
Middle row: S. megistacrolobum.
Back row : S. raphanifolium.

(b) Series Tuberosa
Front row : S. simplicifolium.
Middle row: S. canasense.
Back row : S. famatinae.



(a) (b) (c)



(d) (e)

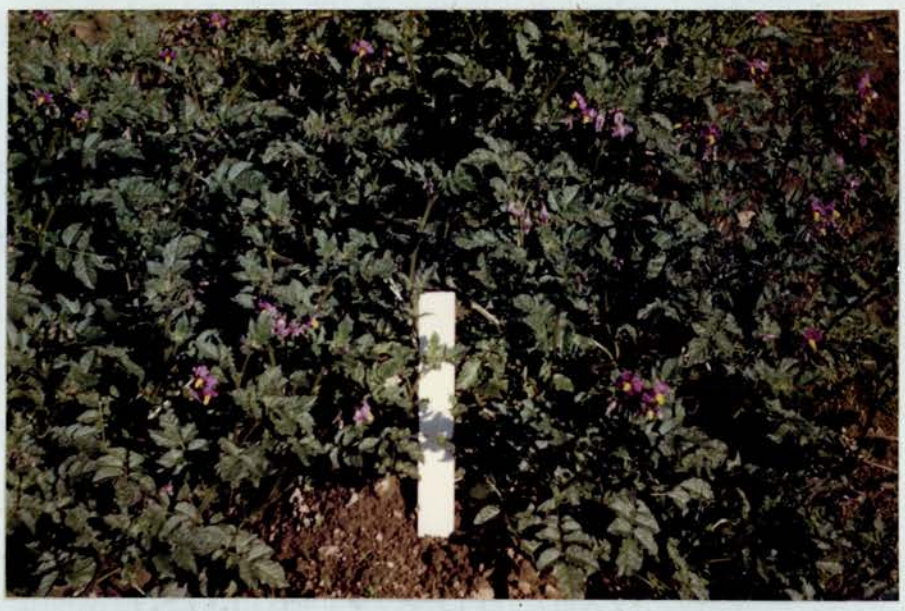
Plate 8. Leaf shape in species of potato resistant to root eelworm.

(a) S. raphanifolium)
(b) S. megistacrolobum) Series Megistacroloba.
(c) S. sanctae-rosae)

(d) S. multidissectum) Series Tuberosa.
(e) S. neohawkesii)

Plate 9. Species of potato resistant to root eelworm
Front row: S. multidissectum
Back row: S. neohawkesii

Plate 10. Progenies of S. multidissectum x S. tuberosum backcrossed to S. tuberosum, growing from cuttings of seedlings under test in the greenhouse. The resistant segregates are available for crossing.



(a)

(b)

Plate 11. The breeding line stemming from S.sanctae-rosae.

(a) Hybrids with S.tuberosum
(b) The first backcross to S.tuberosum

Prolific branching and excessive numbers of small tubers characterise this breeding line.

Regarding the material as a whole, a distinct degree of resistance to the Duddingston population appeared to be the rule rather than the exception in wild species of potato. Most of the more resistant species and crosses could be grouped according to breeding or taxonomic relationships. Some of them, particularly S. sanctae-rosae, may be useful alternatives to S. vernei as sources of resistance to aggressive populations as typified by the Duddingston population.

(3) Interaction between type of resistance and type of pathogenicity

The third group of material was tested in two series of 4-inch pots containing standard quantities of Duddingston and Boghall culture media. The estimated egg populations per pot, the criterion of infectivity, did not differ significantly between series, viz:-

	Eggs/gm.	Egg population per pot
Duddingston series	41.6	29,709 ± 3,300
		P = 0.2
Boghall series	38.7	27,024 ± 1,904

The plants were allowed to dry out after an inspection of root-balls, in preparation for the recovery of cysts from the culture media when air-dry. The data for cyst yield were used in calculating the so-called "cyst efficiences" of selected plants, a statistic adopted by Hesling (1957) to specify the percentage of larvae maturing.

$$\text{cyst efficiency} = \frac{\text{estimated new cysts} \times 100}{\frac{1}{2} \text{ the initial egg population}}$$

Species and control clones	Cyst efficiency											
	Duddingston population										Mean	Boghall population											Mean
71/17	31	32	44	32	31	35	41	39	40	39 38	37	40	37	46	55	48	35	50	49	59	49	55	48
Triploids	1.6	2.6	3.0	4.0	1.4						2.6	18	40	21	29	22							26
S. demissum	1.4	1.4	1.0	1.8	3.6	3.0	1.2	1.2	1.6		2.2	11	16	5.6	17	18	15	21	-	-			14
S. vernei	0	0	0	0	0	0	0	0	0	0 0	-	0	0	0	0	0	0	0	0	0	0	0	-
S. famatinae	4.4	4.2	5.0	-	2.2	2.6					3.4	0	0	0	0	0	0						-
71/1	31	29	26	32	34	21	27	32	19	18	27	0	0	0	0	0	0	0	0	-	-		-

TABLE 5. CYST INDICES OF SELECTED CLONES.

The calculation of cyst efficiency assumes a 1 : 1 sex ratio and permits an assessment of resistance in absolute terms of survival of the parasite. In practice, because of errors in sampling, this assessment is rarely accurate enough to distinguish between plants which remain free from cysts and those which bear few cysts in relation to the number of old cysts present initially in the culture medium. Under these conditions, the direct observation of root-balls yields the more positive information.

The estimates of cyst efficiency which occupy corresponding positions under the different population headings in Table 5 refer to the same clone. When several results appear between vertical separations, all again refer to different plants of the same clone. The means are calculated as between clones. Zero cyst efficiency indicates that the root-balls of these plants were free from cysts. For both populations, an increment of 100 new cysts per 4-inch pot was equivalent to a cyst efficiency of 0.7. As expected, the results for different plants of the same clone were sometimes highly variable, but significant differences between series were apparent from inspection.

The maximum multiplication of both populations occurred in association with the susceptible control clone 71/17. S.vernei remained free from cysts of both populations. The plants of 71/1, having the resistance of subsp. andigena C.P.C.1673, remained free from cysts of the Boghall population, as did the plants of S. famatinae. The resistance of S. famatinae broke down against the Duddingston population, but to a much lesser extent than did the resistance of 71/1. S. demissum and the triploid clones

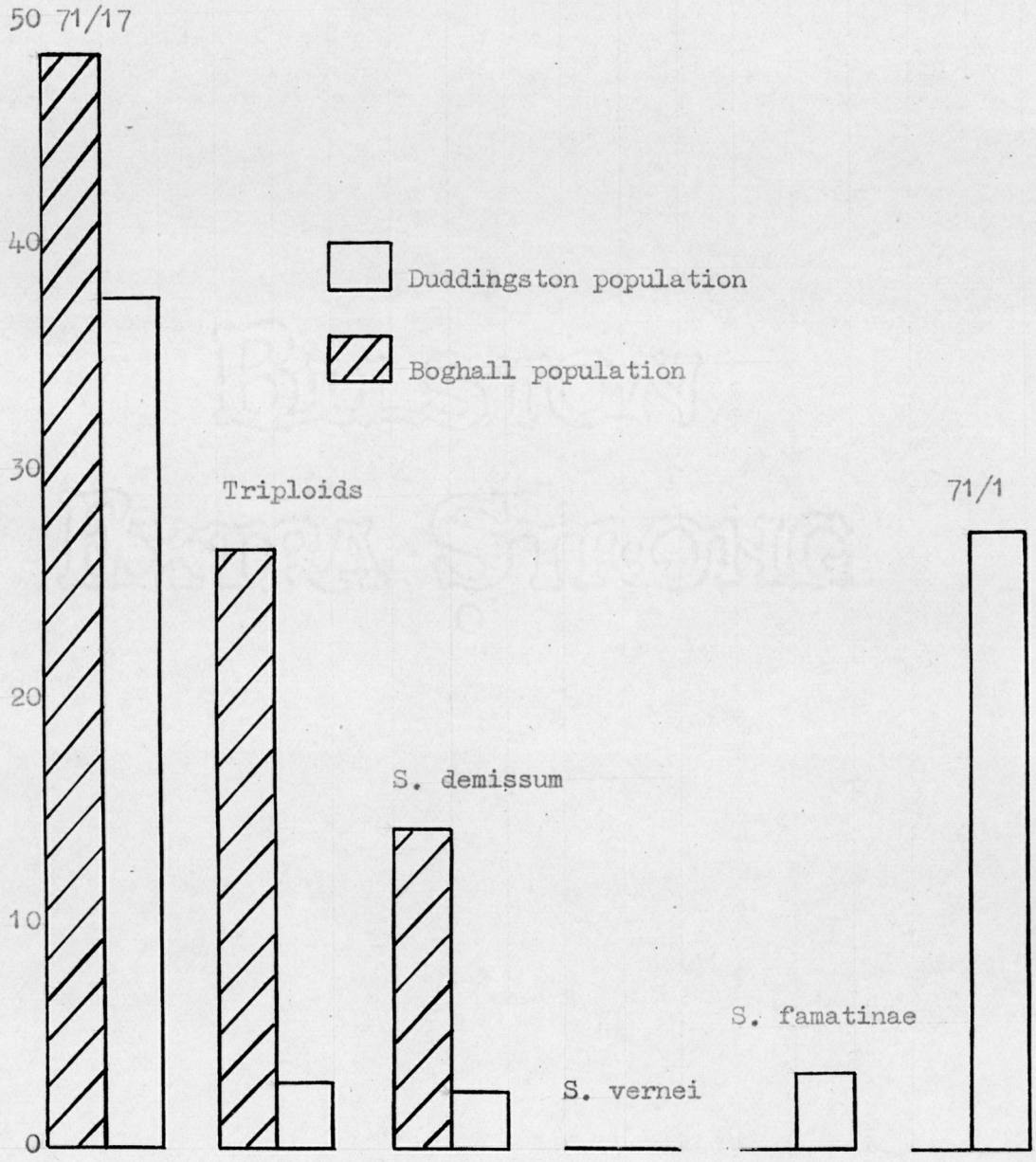


FIG. 4. INTERACTION BETWEEN TYPE OF RESISTANCE AND TYPE OF PATHOGENICITY : COMPARISON OF CYST EFFICIENCIES.

were significantly more susceptible to the Boghall population than to the Duddingston population. This difference in susceptibility was especially obvious in the triploid clones, which yielded nine times more cysts with the Boghall population than with the Duddingston population. The reversal of the aggressive trends in the pathogenicity of the Duddingston and Boghall populations is clearly brought out in Fig. 4, which sums up the results in Table 5.

DISCUSSION

The economic importance of potato root eelworm dates from 1913 when a crop in the region of Rostock was seen to be considerably damaged by the pest (Zimmermann, 1914). Subsequent researches into the host range of the potato root eelworm may be grouped in three phases, so well defined that they may be dated. The first two phases will be passed over briefly.

Phase I. 1913-1940: during this period, the specific identity of the cyst-forming eelworm which attacked potatoes was not fully recognised. Although Wollenweber erected the ~~genus~~ species Heterodera rostochiensis in 1923, many workers continued to regard the eelworm as a strain of the longer established Heterodera schachtii Schmidt, the beet root eelworm. Consequently, considerable powers of adaptation were attributed to what was in effect a composite species. The first phase ended in 1940 when Franklin confirmed the specific status of Heterodera rostochiensis on grounds of detailed morphology.

Phase II. 1940-1955: during this period it was acknowledged that the host range of H. rostochiensis was

restricted to the genus Solanum and the allied genus Lycopersicum. However, the incidence of cysts and rate of multiplication of potato root eelworm varied widely in association with plants of different species, some of which were then said to comprise better hosts than others (Franklin, 1940). The outstanding event of this phase was Ellenby's finding of extremely effective resistance in four clones of S. tuberosum subsp. andigena (1951) and in S.vernei (1948). The second phase ended in 1955, when the andigena type of resistance failed to prevent the multiplication of a population of potato root eelworm from a garden in Edinburgh, (Anon., 1956; Dunnett, 1957). The significance of this finding lay in the predominance of resistance-breaking biotypes in a population which could have had no history of association in Britain with varieties of potato possessing the type of resistance in question.

Phase III. After 1955 the eelworm population, rather than the species, became the unit to be considered in breeding for resistance. The investigations reported in this paper refer to two specified populations of eelworm of different pathogenicity. The Duddingston population was said to be aggressive because the type of eelworm resistance determined by the gene H present in subsp. andigena C.P.C.1673 did not prevent the multiplication of this population. Presence of the same gene ensured virtual freedom from cysts of the Boghall population.

It was seen that the maximum multiplication associated with the susceptible control clone, which belonged to S. tuberosum in the broad sense, was the most obvious factor

in common between the Duddingston and Boghall populations. This was to be expected since any field population of potato root eelworm in Britain must multiply on crops of potatoes in order to survive. With regard to potatoes having the resistance of subsp. andigena C.P.C.1673, S. famatinae, S. demissum and the triploid clones, however, there was evidence of a complex host/parasite relationship in that the two populations were aggressive in different degree towards the different resistant potatoes.

SECTION III.

Errata

Read "cyst index" for "susceptibility index" and "root-ball" for "soil-ball" throughout this Section.

Potato Breeders' Strains of Root Eelworm (*Heterodera rostochiensis* Woll.)

The first phase of breeding for resistance to potato root eelworm was initiated by the finding of resistance in clones C.P.C. 1673, C.P.C. 1685 and C.P.C. 1690 of *Solanum tuberosum* subsp. *andigena* (Ellenby, 1952). However, none possessed uniform resistance to populations from different fields, glasshouses and gardens in Britain (Dunnett, 1957; Jones, 1957). Dunnett (1958) selected clones of *S.vernei* Bitt. et Wittm., *S. multidissectum* Hawkes and *S. sanctae-rosae* Hawkes, three diploid species of potato, as potentially useful sources of resistance to the so-called Duddingston population of potato root eelworm maintained at the Scottish Plant Breeding Station and characterised by aggressiveness towards plants possessing the resistance of subsp. *andigena* C.P.C. 1673. The latter type of aggressiveness distinguished the Duddingston population from the Boghall population, also maintained at the Scottish Plant Breeding Station. Further study showed that the Boghall population was aggressive towards plants possessing the resistance which was present in the selected clones of *S. multidissectum*. The selected clones of *S. vernei* and *S. sanctae-rosae* were equally resistant to both populations. These findings prompted the following enquiry into the status of physiological strains of the eelworm and the possibility of investigating the relationship between genes controlling pathogenicity in the eelworm and genes controlling resistance in potatoes.

The selective culture of breeders' strains of the potato root eelworm

A selective host for an aggressive population of the eelworm may be defined as a clone or variety of potato possessing resistance which virtually precludes the survival of biotypes lacking a particular type of aggressiveness regarded as the distinguishing feature of the population. Consequently, plants possessing the resistance of subsp. andigena C.P.C.1673 can be regarded as selective hosts for the Duddingston population, which has been multiplied annually for the past four years on plants having this type of resistance. Therefore, the present Duddingston population can be denoted by Duddingston x 4 (C.P.C.1673) and population x n (selective host) denotes the general case.

The efficiency of selective culture is greatest if cysts containing an unhatched residue of viable eggs of the parental generation do not mingle with those of their progeny. Separation can be achieved by using prehatched larvae as inoculum or by enclosing the parental cysts in a wire basket of appropriate mesh (Ellenby, 1955).

If recessive aggressiveness is postulated, a population composed solely of biotypes homozygous for aggressiveness is achieved when n = 1, provided (a) that one of the foregoing techniques for selective culture is employed and (b) that the survival of males and females is dependent on the same genetic factors, in which case only recessive males would survive to fertilise the recessive females. If dominant aggressiveness is postulated and an equal frequency of the gene A for aggressiveness and the gene a for non-aggressiveness

is assumed initially, then random mating in a selectively cultured population of unlimited size results in the following trend towards homozygous aggressiveness:- population x n (selective host) = $(n + 1)^2$ AA + 2 (n + 1) Aa + 1aa.

This is an adaptation of the formula given by Dice (1940) in a paper on the elimination of lethal characters in populations. By analogy with Dice's exposition the trend towards homozygosity would take place at approximately the same rate whether aggressiveness were controlled either by multiple dominant factors or by a single dominant gene, as instanced above. If some of the multiple factors were recessive, the trend towards homozygosity would be more pronounced.

Granted that a particular population of the eelworm is composed almost entirely of biotypes which are aggressive towards a particular selective host, a true measure of aggressiveness is the probability of a given biotype surviving to female maturity in the selective host. Prolonged selective culture will not increase the rate of multiplication of a population which is already homozygous for a low degree of aggressiveness unless mutation in the direction of increased aggressiveness takes place.

An aggressive population which is subjected to selective culture may be regarded justifiably as a breeders' strain of the eelworm but the classification of different strains, each having a different selective host, is complicated by the fact that resistance or aggressiveness must be measured against a continuous scale. It is proposed to restrict the differential

host series to plants possessing at least a certain "standard" level of resistance to one or more strains, to ensure that the classification is the basis of a practical scheme for controlling potato root eelworm by varietal resistance in potatoes.

A standard level of resistance to eelworm

The clone C.P.C.1673 of subsp. andigena incorporated a dominant gene, designated H by Toxopeus and Huijsman (1953), which conferred resistance to eelworm. Even before the finding of aggressive populations of the eelworm in Britain, there was abundant evidence that cysts arose occasionally on plants of genotype H, (Toxopeus and Huijsman, 1953; Jones, 1954; Williams, 1956; Cole and Howard, 1957): in particular, "occasional" cysts were observed on the resistant plants exposed to infection by the Boghall population of the eelworm (Dunnett, 1957). The latter relationship was further studied to establish a practical basis for the measurement of a "standard" level of resistance to eelworm, corresponding to the level of resistance which was available to potato breeders during the first phase of breeding for resistance to eelworm.

Two plants of each of 171 resistant clones were grown in 4-inch pots of soil containing 40 eggs/gm. and forming two series (Series I and II). Fifty plants of a resistant clone comprised Series III and ten plants of the commercial variety, Kerr's Pink, were used to follow the development of cysts on roots. The pots were sunk to the rim in the ground.

Class: No. of cysts	0	1	2	7	10	40	Totals	Failed
Frequencies, test plants								
Series I	151 92%	11 6.7%	1 0.7%	0	0	0	163	8
Series II	141 89.8%	12 7.6%	2 1.3%	0	1	1	157	14
Frequencies, control plants								
Series III	44 95.6%	1 2.2%	0 0%	1	0	0	46	4
Expected frequencies								
Poisson distribution	90%	9.5%	1.4%					
Class: No.of cysts	*0,0	0,1	0,2		0,10	1.40		
Frequency of pairs of results from Series I and II	124	21	2		1	1	149	22

* 0,0 = no cysts observed on either plant of a pair,
0,1 = none on one and one on the other and so on.

TABLE 6. THE INCIDENCE OF CYSTS ON TEST AND CONTROL PLANTS

After ten weeks, when the cysts on Kerr's Pink were yellow or orange in colour, the resistant plants were removed from the pots and cysts attached to the undisturbed root mats in an exposed position were counted. The results are given in Table 6.

It can be deduced from Table 6 that when one or more cysts occurred on any plant in Series I and II combined, the probability of detecting one or more cysts on the other plant of the pair (P = 4%) was less than that of detecting one or more cysts on a plant chosen at random from either series (P = 7% and 10%). Since there was no tendency for cysts to occur on pairs of plants it was concluded that the clones did not differ in their susceptibility to "occasional" cysts.

Table 6 showed that the level of resistance to the Boghall population conferred by the gene H could be specified accurately as the level of resistance which resulted in 90% of the infected plants remaining cyst-free. Therefore, if all the biotypes in the Boghall population were uniform in pathogenicity towards plants of genotype H, or if aggressive biotypes were uniformly distributed throughout the population as a whole, then the percentage frequency of plants bearing no cysts, one cyst, two cysts and so on should fit the hypothetical Poisson distribution. If the occurrence of 7, 10 and 40 cysts on three of the resistant plants is omitted, agreement is reasonable. Probably the pots in which these three plants were grown had contained at least one cyst which had given rise to a family of aggressive larvae.

Scale of resistance to eelworm

Clones	resistance	sign	
Group 1	above standard	-	all plants of a clone have cyst-free soil-balls.
		•	90 per cent of the plants of a clone have cyst-free soil-balls
Group 2	near standard	±	Mean count of 10 cysts per soil ball (equivalent to a susceptibility index of 2 cysts per 100 windows-with-roots).
Group 3	below standard	+	250 cysts per 100 windows-with-roots, maximum recorded susceptibility index.

The level of resistance determined above was regarded as the "standard" level of resistance to aim at in new varieties of potato. Thus 90% of the plants of a clone or variety possessing standard resistance remain cyst-free on the basis of an inspection of root-balls after exposure to infection from cysts in 4-inch pots containing a culture medium of 40 eggs/gm. infectivity. The incidence of cysts on the remaining 10% is immaterial to this definition. The type of culture medium in use at the Scottish Plant Breeding Station is prepared by mixing air-dried, infested soil of particle size less than 0.1 inches with coarse sand. The volume of sand required to reduce infectivity to 40 eggs/gm. is usually 10-15 times the volume of soil. The pots are sunk to the rims in an electrically heated sand plunge. This method of sand culture superseded the soil culture in use at the time of the investigation reported above. The change in conditions has had no appreciable effect on the incidence of "occasional" cysts on plants of genotype H.

Standard resistance is the first of two intermediate points in the accompanying, continuous scale of resistance to eelworm. A mean count of ten cysts on the plants of a clone is the second point. The latter point was selected (a) because it was considered that clones in group 2 might be useful for breeding purposes in certain instances, particularly if the near standard resistance were controlled by a single gene and (b) because group 2 (±) created a marked discontinuity between group 1 (-) and group 3 (+). For tabulating strain relationships (Table 9) the minus sign means "resistant" or

"non-aggressive" depending on the point of view and the plus sign means "susceptible" or "aggressive". The ± sign indicates an intermediate or doubtful strain reaction. Group 3 covers a very wide range of resistance as reflected by the difference between a mean count of 10 cysts and the recorded maximum of 1,000 - 1,250 cysts observed to date over the surface of a 4-inch root-ball under the conditions appropriate to the assessment of standard resistance. The perforated can method (Dunnett, 1957) is used to assess variation in level of resistance within group 3 and counts of 10 cysts or more are expressed in the form of a cyst index.

The resistance to eelworm of Solanum vernei, S. sanctae-rosae and S. multidissectum

Dunnett, (1960), concluded that the resistance of S. vernei to both the Duddingston and Boghall populations was above standard and controlled by a system of polygenes.

Resistance to the Duddingston population in S. multidissectum and S. sanctae-rosae was detected in 1956 (Dunnett, 1958). The progeny of S. sanctae-rosae (P.H.328) comprised four seedlings free from cysts and one seedling bearing one visible cyst. The progeny of S. multidissectum (P.H.1366) comprised five seedlings free from cysts and one seedling which supported six visible cysts. More than 200 cysts were visible on the control plants under the same conditions. Subsequently, three cyst-free seedlings were selected from each progeny and were grown on to yield tubers. The selected seedlings were now clones and crosses were made between clones of the same species. In 1957, up to six plants of each clone

Cysts per 100 windows-with-roots		(a) Boghall population			(b) Duddingston population		
Control clone (genotype H)							
71/1	(a)	0(F)	0(F)	0(F)	0(F)	0(F)	0(F)
	(b)	72	82	93	103	106	123
S. multidissectum							
Clone 14/2	(a)	3	3	3	5	6	-
	(b)	0(F)	0(F)	0(F)	0(F)	0(F)	0(F)
Clone 14/4	(a)	0(2)	0(2)	2	2	4	5
	(b)	0(F)	0(F)	0(F)	0(F)	0(F)	0(F)
Clone 14/5	(a)	0(4)	3	4	10	14	14
	(b)	0(F)	0(F)	0(F)	0(F)	0(F)	0(F)
S. sanctae-rosae							
Clone 4/2	(a)	0(F)	-				
	(b)	0(F)	0(F)				
Clone 4/4	(a)	0(F)	0(F)	0(F)	0(F)	-	-
	(b)	0(F)	0(F)	0(F)	0(F)	0(F)	0(F)
Control clone (genotype h)							
71/17	(a)	72	82	93	102	106	123
	(b)	150	153	180	199	237	245

(F) = free from cysts: (1, etc.) = cysts observed over whole soil-ball surface.

TABLE 7. CYST INDICES OF CLONES

Species and Control clones	Number of cysts								
	0	1-2	3-5	6-11	12-24	25-49	50-99	100-200	200+
	Progenies infected by Boghall population								
S. sanctae-rosae	45	0	0	0	0	0	0	0	0
S. multidissectum	0	10	5	11	4	4	7	0	0
71/1 (genotype H)	8	0	0	0	0	0	0	0	0
71/17 (genotype h)	0	0	0	0	0	0	0	6	2
	Progenies infected by Duddingston population								
S. sanctae-rosae	43	0	0	0	0	0	0	0	0
S. multidissectum	47	3	0	0	0	0	0	0	0
71/1 (genotype H)	0	0	0	0	1	1	5	1	0
71/17 (genotype h)	0	0	0	0	0	0	0	8	0

TABLE 8. DISTRIBUTION OF SEEDLINGS ACCORDING TO CYST COUNT IN PROGENIES DIVIDED BETWEEN THE BOGHALL AND DUDDINGSTON POPULATIONS.

were tested against the Boghall population and an equal number were tested against the Duddingston under the conditions already laid down for assessment of standard resistance. The gene H from subsp. andigena C.P.C. 1673, was present in the resistant control clone 71/1 but not in the susceptible control clone 71/17, which was about equally susceptible to both populations.

The susceptibility indices recorded are given in Table 7 together with the number of cysts on the root mat, if ten cysts or fewer were present. Resistance in the three clones of S. sanctae-rosae to both populations was above standard. The resistance of the three clones of S. multidissectum to the Duddingston and Boghall populations was above standard and below standard, respectively. The Boghall population was less aggressive towards S. multidissectum than was the Duddingston population towards the control clone incorporating the gene H. Judging from the susceptibility indices of the susceptible control clone, conditions seem to have been more conducive to cyst formation in the Duddingston series.

In 1957, to compensate for the shortage of clonal material, 100 seedlings of S. sanctae-rosae and 100 seedlings of S. multidissectum were tested for resistance to the Boghall and Duddingston populations. Table 8 records the distribution of these seedlings and plants of the control clones, according to the estimated number of cysts observed over the surfaces of soil-balls from 3-inch pots. The results supplement those of Table 7.

In 1958, a distinct segregation of resistance to the Duddingston population was apparent in a progeny of parentage S. multidissectum (unreduced gametes) x S. tuberosum. Ten of the seedlings remained free from cysts, one seedling supported one cyst, and the remaining seedling had a susceptibility index of 24 cysts per 100 windows-with-roots. The Duddingston population multiplied 5.6 times on the last seedling and declined by four-fifths in pots with the other seedlings.

In 1959, there was evidence of undiminished resistance in the first backcross of the hybrids with S. multidissectum to S. tuberosum. Resistance was dominant and by replicating some of the first backcross families it may be possible to establish whether or not there is complete discontinuity between the resistant and susceptible classes.

Also in 1959, there was evidence of polygenic inheritance of resistance to the Duddingston population in crosses between S. sanctae-rosae (4n) and S. tuberosum, although the hybrids appeared to be less uniform in resistance than the hybrids between S. vernei (4n) and S. tuberosum.

In resistance S. multidissectum can be classed with S. tuberosum subsp. andigena, clone C.P.C. 1673. Both species are sources of the standard level of resistance to certain specified populations of the eelworm only, and the resistance is conferred by one or few genes. The resistance of subsp. andigena C.P.C.1673 is not dependent on the failure of larvae to hatch at a normal rate in the vicinity of the root systems of the resistant plants (Williams, 1957), and

the same is apparently true of the resistance in S. multidissectum. The latter species is indigenous to Peru and Bolivia (Bazàn de Segura, 1952; Bell and Alandia, 1955), which is also the known distribution of the eelworm in South America.* There are no cultivated varieties of S. multidissectum but many varieties of subsp. andigena are cultivated in the Andean highlands including parts of Peru and Bolivia, where the clone C.P.C.1673 was collected. A Peruvian population of the eelworm proved to be aggressive towards plants having the resistance of C.P.C.1673 (Quivedo Díaz et al, 1956) and was, therefore, akin to the Duddingston population in pathogenicity. S. multidissectum possesses the standard level of resistance to the Duddingston population.

These facts suggest that a type of resistance to eelworm may be advantageous to a species of potato exposed to eelworm attack and that pathogenic adaptation in the eelworm will tend to negate the advantage eventually.

S. sanctae-rosae can be classed with S. vernei, in that the resistance of both species appears to be polygenic and proof against known variation in the pathogenicity of the eelworm. Williams (1956) noted that the resistance of S. vernei was associated with a lower rate of hatching than was the resistance of subsp. andigena C.P.C.1673, and fewer larvae entered the root systems of the resistant plants. S. vernei and S. sanctae-rosae may occupy a position at the fringe of the eelworm's host range, a position which perhaps owes more to the process of speciation within the tuber-bearing section of the genus Solanum than to natural selection for

* Transpose reference to position indicated.

	Strain of *H. rostochiensis* / Differential host Series	Clone 71/17 "universal host"	subsp. *andigena* C.P.C.1673 clone 71/1, genotype H	*S.* multidissectum clone 14/5	*S.* multidissectum x clone of genotype H
a	Nonaggressive	(+)	(-)	(-)	(-)
b	Boghall	+	-	+	?
	Dudding ston x 4 C.P.C.1673	+	+	-	?
c	Boghall + Dudding ston x 4 C.P.C.1673	+	+	+	?

\+ resistance below standard - resistance standard or above standard

TABLE 9. TABULATION OF STRAIN RELATIONSHIPS

resistance to eelworm. It may be significant that S. vernei and S. sanctae-rosae are limited in distribution to Argentina (Hawkes, 1956), where the eelworm is not yet reported to occur.

Strain relationships.

In theory, Heterodera rostochiensis may be subdivided as follows:-

(a) populations containing few or no aggressive biotypes.

(b) populations composed entirely or almost entirely of biotypes characterised by a particular type of aggressiveness, negating a particular type of resistance.

(c) populations intermediate between (a) and (b) or intermediate between populations of different pathogenicity classed under (b).

Group (a) is the nonaggressive strain of the eelworm. Group (b) comprises the aggressive strains, each of which has a selective host as previously defined. A population in group (c) is representative of no particular strain but may be regarded as a mixture of strains. Such a mixture may be resolved in the direction of a breeders' strain of the eelworm by selective culture on a selective host, or the mixture may be perpetuated by non-selective culture on a neutral host, in contra-distinction to a selective host.

Group (a) in Table 9 is hypothetical and must remain so until a representative population is obtained direct from the field, since by definition the nonaggressive strain cannot be cultured selectively. Group (b) is represented by the Boghall strain, which will be selectively cultured in future

on plants having the resistance of S.multidissectum in an effort to increase the aggressiveness of this strain. Group (b) also includes the Duddingston strain which already has a history of selective culture, expressed by writing Duddingston x 4 C.P.C. 1673, and which multiplies from 20 to 30 times on plants having the resistance of subsp. andigena C.P.C.1673. The pathogenicity of the Duddingston population is the antithesis of the pathogenicity of the Boghall population in that neither population contains more than a negligible proportion of biotypes capable of surviving to female maturity in the selective host of the other population. The selective culture of Duddingston x 4 C.P.C.1673 may have been partially responsible for this relationship.

Group (c) in Table 9 is represented by a mixture of the Boghall and Duddingston strains. Such a mixture has already been multiplied on a neutral host and the resulting population will be selectively cultured on plants possessing the combined resistance of subsp. andigena C.P.C. 1673 and S. multidissectum. The objective is the formation of a new strain which will negate the genetic combination of both types of resistance. The search for a new type of resistance can then begin.

S. vernei and S. sanctae-rosae are excluded from Table 9 because hybridisation with S. tuberosum, the first step in breeding, gives diminished resistance due to polygenic inheritance and there seems little possibility of establishing the relationship between strains and designated genes in these species.

The range of genetic variability in naturally occurring populations is probably greater than in selectively cultured strains descended from relatively few aggressive biotypes. By using strains of minimum variability, perhaps even strains descended from a single aggressive female, the breeder can hope to distinguish with the greatest possible precision between kinds of resistance to potato root eelworm in the many species of potato indigenous to South and Central America.

Unless immunity from potato root eelworm or a type of resistance which always suppresses cyst formation can be incorporated in new varieties of potato, the problem of controlling the eelworm by varietal resistance is a problem of strains. Separate infestations can be treated as separate problems. The answer to these problems is an appropriate rotation of different resistant varieties at suitable intervals in particular fields. Although there appears to be no lack of resistance in the tuber-bearing Solanums it may be many years before a range of different types of resistance is available in commercial varieties of potato.

SECTION IV.

The role of *Solanum vernei* Bitt. et Wittm. in breeding for resistance to potato root eelworm (*Heterodera rostochiensis* Woll.)

Solanum ballsii was described from material collected by Hawkes and Balls in Northern Argentina in 1939 (Hawkes, 1944). Subsequently, Hawkes compared *S. ballsii* in the Commonwealth Potato Collection (C.P.C.) at Cambridge with *S. vernei* in the Erwin Baur Collection (E.B.S.) of the Max Planck Institute, Cologne, and referred (1956) to *S. vernei* subsp. *ballsii*, based on *S. ballsii*. The E.B.S. stock of *S. vernei* was acquired from Brücher, who rediscovered the species in Northern Argentina in 1950, thirty-six years after the original collection by Wittmack (Goffart and Ross, 1954). Brücher (1957) found no evidence to support the retention of *S. ballsii* as a sub-specific name.

S. vernei is not a cultivated species but is a probable ancestor of cultivated potatoes of the "*S. andigenum* group" (*S. tuberosum* L.) according to Brücher (1954).

Ross and Baerecke (1951) detected "incubation resistance" to *Phytophthora infestans*, the late blight fungus, resistance to potato virus Y and resistance to frost in *S. vernei*.

The resistance of S. vernei to potato root eelworm. Ellenby reported (1948) that the C.P.C. stock of *S. vernei* was resistant to potato root eelworm. Larvae were present in the roots of the plants exposed to infection, but even immature cysts were very rare. Ellenby's findings were confirmed in the U.S.A. by Mai and Peterson (1952) who

Plate 12. Solanum vernei.
Left : Diploid.
Centre: Colchicine-induced tetraploid, with broader leaflets than the diploid.
Right : Colchicine-induced octoploid, dwarf and distorted.

Plate 13. Hybrid between S.vernei (4n) and S.tuberosum, closely resembling S. tuberosum in foliage.

worked with material obtained from Cambridge. Macdonald (1956), also working in the U.S.A., recovered mature cysts from S. vernei of unspecified origin. Goffart and Ross (1954) and Rothacker (1957) found the E.B.S. stock of S. vernei to be outstandingly resistant, although the plants were not always free from cysts. Rothacker (1957) listed a "susceptible" clone of S. vernei. Williams (1958) compared S. vernei with resistant clones bred from S.tuberosum subsp. andigena and found that the plants of S. vernei produced a much less active root diffusate, and were invaded by fewer larvae, of which very few developed past the second or invasive stage, and adults of both sexes were absent. Dunnett (1957, 1958) found that C.P.C. and E.B.S. stocks of S. vernei remained virtually free from cysts and certainly free from cysts past the white stage of development, when infected by either the Boghall or Duddingston populations of the eelworm maintained at the Scottish Plant Breeding Station. These populations differed in pathogenicity towards plants possessing the resistance of subsp. andigena C.P.C. 1673, the Duddingston population being the aggressive population. Jones (1957) reported S. vernei resistant to thirty-seven populations,against most of which the subsp. andigena type of resistance was known to be more or less ineffective. Dunnett (1958) tested P and H 351, a new collection of S. vernei made by Peterson and Hjerting,and observed no cyst formation on six clones infected by the Duddingston population.

Therefore, the resistance of S. vernei is equally effective against the two types of pathogenicity detected to date in naturally occurring populations of H.rostochiensis.

Susceptible clones occur exceptionally, although none have been found in the C.P.C. stock of the species. The cysts which arise occasionally on the resistant clones are usually small and white: conversely the "occasional" cysts found on resistant clones bred from subsp. andigena are usually fully grown and contain eggs. Recent work (Ellenby, 1957; Fassuliotis, 1957; Williams, 1957) has shown that fertilisation is essential for egg production. It is significant that the development of both sexes is equally inhibited in S. vernei whereas an excess of males over females matures in resistant plants bred from subsp. andigena (Jones, 1954; Williams, 1958).

Inheritance of resistance.- Goffart and Ross (1954) postulated polygenic inheritance of resistance in crosses between colchicine-induced tetraploid clones of S. vernei and S. tuberosum, with a tendency for resistance to be dominant. Rothacker (1959) took the same view and suggested that resistance might be due to one or two genes with modifiers. Goffart (1957) mentioned a breeding line stemming from S. vernei which was discontinued because resistance decreased as breeding progressed. At Pentlandfield, the hybrids between S. vernei (4n) and S. tuberosum retained a high level of resistance to the Duddingston population but none remained free from cysts. The infectivity of the Duddingston population declined to four-fifths of the initial level of infectivity in the culture medium in which the most resistant hybrid progeny had grown.

A comparison of breeding lines.- The polygenic resistance of S. vernei is a disadvantage for breeding

purposes because hybridisation with commercial varieties of S. tuberosum, the first step in breeding, results in some loss of resistance throughout the F_1. It is necessary to select and intercross the more resistant seedlings in the more resistant progenies after crossing with S. tuberosum if a variety of potato possessing a standard level of resistance derived from S. vernei is the objective. There is a better prospect of incorporating the resistance of subsp. andigena C.P.C.1673 and S. multidissectum in commercial varieties of potato because segregates with a standard level of resistance occur in the backcrosses to S. tuberosum.

A second disadvantage of S. vernei is the fact that the resistant plants do not stimulate a high rate of larval emergence from cysts in the soil and therefore lack an essential feature of a successful "trap crop" for potato root eelworm. Plants having the resistance of subsp. andigena C.P.C.1673 possess this "trap cropping" property to a much higher degree.

Despite these disadvantages, S. vernei may still play an important role in breeding for resistance to potato root eelworm. The scope of the resistance in relation to variation in the pathogenicity of H. rostochiensis may be broader than that of subsp. andigena C.P.C.1673 and S. multidissectum, since no populations aggressive towards S. vernei are known at present. Until aggressiveness towards S. vernei can be demonstrated, the species must be regarded as almost outside the host range of H. rostochiensis and the resistance may be proof against the whole range of possible variation in

the pathogenicity of the pest. This kind of resistance would be very valuable and comparable in significance to the polygenic "field resistance" (Black, 1960) of Solanum demissum to Phytophthora infestans, the fungus causing late blight of potatoes. Even part of the resistance of S. vernei combined with resistance to particular strains conferred by dominant genes derived from subsp. andigena C.P.C.1673 and S. multidissectum, might delay the evolution of new aggressive strains of potato root eelworm.

SECTION V.

INHERITANCE OF RESISTANCE TO THE DUDDINGSTON STRAIN IN THE BREEDING LINE STEMMING FROM S. MULTIDISSECTUM

The segregations of resistant and susceptible seedlings through three generations is given in Table 10, the record of all progenies tested during this phase of breeding. The tests were conducted in 3-inch pots containing plants raised from true seed. The B_1 and B_2 progenies comprised 48 and 54 seedlings respectively, excepting progeny 4095 with a total of 36 seedlings. The number of seedlings which failed to yield a result never exceeded four in progeny. Scoring was based primarily on presence or absence of cysts on root-balls, although 9.4 and 8.9 per cent. of the resistant segregates in generations B_1 and B_2, respectively, were seen to support up to 5 cysts ("occasional cysts"). On this basis, the resistant class as a whole could be said to possess the standard level of resistance, although strictly speaking the definition of standard resistance (page 62) stipulated 4-inch pots.

The susceptible class comprised 50.0 per cent. (B_1) and 53.3 per cent. (B_2) seedlings that were considered to be less than fully susceptible, although distinct from seedlings with "occasional cysts".

The F_1 generation comprised 11 hybrids obtained by pollinating a diploid clone of S. multidissectum, grown under glass, with pollen from a tetraploid breeding clone of S. tuberosum. These and subsequent hybrids resulting from the same cross were invariably tetraploid and up to 39 were obtained from the same berry. The hybrids were presumed to result from the union of unreduced female gametes of

Generation	Progeny reference	Resistant parent	Segregations resistant:susceptible	Hypothetical ratio	Chi-square for difference from expectation	P
F_1	3246	S. multidissectum	11 : 1	1 : 1		
B_1	3486	3246/ 2	8 : 35	all susceptible		
	3487	3246/ 3	38 : 9	5 : 1		
	3488	3246/ 4	35 : 7	5 : 1		
	3490	3246/ 5	45 : 3	5 : 1	3.04†	0.05-0.1
	3491	3246/ 6	37 : 7	5 : 1		
	3492	3246/ 7	31 : 14	5 : 1	5.76†	0.01-0.02
	3493	3246/ 8	0 : 47	all susceptible		
	3495	3246/ 9	35 : 5	5 : 1		
	3497	3246/11	32 : 13	5 : 1	4.00†	0.02-0.05
	3498	3246/12	40 : 6	5 : 1		
	3499	3246/13	40 : 8	5 : 1		
	Sum of presumed 5:1 segregations		333 : 72	5 : 1	0.36	0.50-0.70
B_2	4067	3487/19	23 : 28	1 : 1		
	4069	3487/40	29 : 25	1 : 1		
	4070	3488/10	33 : 20	1 : 1		
	4071	3488/18	33 : 19	1 : 1	3.25†	0.05-0.10
	4073	3488/35	34 : 10	5 : 1	0.79†	0.30-0.50
	4078	3490/40	27 : 27	1 : 1		
	4079	3490/41	43 : 7	5 : 1		
	4081	3490/46	20 : 15	1 : 1		
	4082	3491/ 5	25 : 29	1 : 1		
	4083	3491/43	35 : 4	5 : 1		
	4084	3492/44	25 : 29	1 : 1		
	4085	3495/12	45 : 9	5 : 1		
	4086	3495/18	24 : 28	1 : 1		
	4089	3497/ 5	45 : 9	5 : 1		
	4090	3497/24	26 : 24	1 : 1		
	4091	3498/ 1	24 : 28	1 : 1		
	4095	3498/19	16 : 17	1 : 1		
	4098	3499/24	27 : 26	1 : 1		
	4101	3499/47	50 : 4	5 : 1		
	Sum of presumed 5:1 segregations		252 : 43	5 : 1	0.23	0.50-0.70
	Sum of presumed 1:1 segregations		332 : 315	1 : 1	0.44	0.50-0.70

F_1 = S. multidissectum x S. tuberosum. B_1 = First backcross to S.tuberosum. B_2 = Second backcross

† calculation including Yates's correction for continuity.

TABLE 10. SEGREGATIONS IN THE BREEDING LINE STEMMING FROM S. MULTIDISSECTUM.

S. multidissectum with ordinary diploid gametes of S. tuberosum. If so, the incidence of unreduced gametes was exceptionally high.

The resistant parents of the B_1 and B_2 generations were pollinated in the field and were always emasculated. The emasculated flowers were not covered to prevent visits by insects because bagging adversely affected the set of berries and it was known from experience that there was only a small risk of effective cross pollination by insects.

The data as a whole (Table 10) supported the hypothesis that the resistance was mainly conferred by a dominant gene.

For present purposes, this dominant or major gene can be designated simply by R signifying "resistant". The resistant, tetraploid parents were apparently either duplex or simplex, giving the following hypothetical segregations (autosyndesis) in crosses with nulliplex commercial varieties of S. tuberosum.

Cross	Progeny	Segregation resistant : susceptible
simplex (Rrrr) × nulliplex (rrrr)	1 Rrrr : 1 rrrr	1 : 1
duplex (RRrr) × nulliplex (rrrr)	1 RRrr : 4 Rrrr : 1 rrrr	5 : 1

~~Only~~ None of the nineteen segregations in the B_2 generation differed significantly from the expected ratios of either 1 : 1 or 5 : 1 and the summations separately of the approximate 1 : 1 and 5 : 1 segregations gave low values of chi-square, indicative of close agreement with expectation. In addition the number of approximate 5 : 1 segregations (6) and approximate 1 : 1 segregations (13) was near to 4 : 15, this

being the nearest possible approach to a 1: 4 ratio based on the assumption that the resistant B_1 parents of the B_2 generation were themselves selected from duplex x nulliplex crosses (giving 1 RR to 4 Rr and a segregation of 5 resistant : 1 susceptible). In fact, nine of the eleven B_1 progenies segregated approximately 5 : 1 although there was a significant excess of susceptibles in two of the progenies (3492 and 3497). The progeny 3497 contained at least one duplex segregate, however, since 3497/5 gave a B_2 progeny which segregated 5 : 1, thus helping to establish that the resistant F_1 parent of 3497 was also duplex.

Therefore, on the basis of the B_1 progeny tests, at least nine of the original twelve F_1 hybrids were duplex. The only known susceptible segregate (3246/8) in the F_1 gave a wholly susceptible B_1 progeny and was obviously nulliplex. No progeny was obtained from one other hybrid, leaving only one of the twelve unaccounted for. This was 3246/2, which remained cyst-free in a repeat test of resistance, but which gave a predominantly susceptible B_1 progeny (3486). It was concluded that this seedling was nulliplex and that lack of resistance due to the absence of the R gene was masked by a high level of residual resistance which was then largely dissipated in the B_1 cross.

It was deduced, therefore, that the diploid clone of S. multidissectum was heterozygous and had produced unreduced gametes which were either RR or rr. Since there could be no obvious explanation for an unequal production of these gametes, the fact that at least nine out of twelve hybrids carried the gene R was attributed to chance deviation from a

Progeny	Boghall strain			Duddingston strain		
	No.of seedlings	Range of cyst index	Mean	No. of seedlings	Range of cyst index	Mean
3486	26 r	35 - 259	125	32 r	0 - 89	25
3490	1 r		212	1 r		13
	37 R	5 - 150	62	44 R	all cyst-free or "occasional cysts"	0
3492	10 r	57 - 189	121	11 r	6 - 68	28
	16 R	4 - 134	45	21 R	all cyst-free or "occasional cysts"	0
71/17, control clone	6 r	145-252	190	10 r	91 - 195	134

R = resistant r = susceptible

TABLE 11. CYST INDICES IN SEGREGATING PROGENIES DESCENDED FROM S. MULTIDISSECTUM AND INFECTED BY THE DUDDINGSTON POPULATION

1 : 1 hypothetical ratio, a fortunate deviation from the point of view of breeding for resistance.

The progenies 3486, 3490 and 3492 were re-grown from tubers and one plant of each clone was tested against each of the Boghall and Duddingston strains in two series of 4-inch pots containing culture medium of 40 eggs/gm. infectivity. The cyst indices are given in Table 11.

Only one resistant segregate and one susceptible segregate were found to have been classified wrongly a year before when the progenies were first scored for resistance to the Duddingston strain. The segregations given for 3490 and 3492 in Table 10 are the amended segregations. These progenies were selected for re-test because they contained the highest and lowest proportions of resistant segregates in the B_1 generation.

The progeny 3486 had a mean cyst index with the Duddingston strain which was less than a quarter of that for the control clone 71/17 infected by the same population, and the two ranges of cyst index did not overlap. Only one plant of 3486 remained cyst-free, confirming the absence of resistant segregates in this progeny. All the susceptible segregates in 3490 and 3492 had cyst indices within the range recorded for 3486. This established the presence of residual resistance in all three progenies in the absence of the R gene. Since the level of residual resistance appeared to be variable and all but one of the plants of 3486 were clearly less resistant than their resistant F_1 parent (3246/2) a polygenic basis is suggested at present for the residual resistance to the Duddingston population.

This polygenic resistance was almost completely ineffective against the Boghall strain, because now the plants

lacking the R gene and the control clone 71/17 had very similar cyst indices.

Plants of genotype R varied very widely in cyst index with the Boghall strain. Some were clearly as susceptible as the control clone 71/17, while others appeared to have resistance of the order of the residual resistance to the Duddingston strain. It was deduced that the R gene, in the simplex condition at least, did not confer resistance to the Boghall strain. The resistance of some plants of genotype R to this strain requires further investigation to determine the effect of the gene R in the duplex condition and to determine whether or not the R gene in combination with other genes gives resistance due to a complementary effect.

Suggested designation of resistance genes and strains.

The following suggestions will be put forward for consideration by potato breeders working with potato root eelworm.

It is proposed that the gene H of subsp. andigena C.P.C. 1673 should be designated H_1 in future and the major gene of S. multidissectum H_2. The Duddingston strain, aggressive towards potatoes of genotype H_1 only, would then be an example of strain 1. Similarly, the Boghall strain would be an example of strain 2. The genetic combination of resistance would be H_1H_2 and a strain aggressive towards potatoes of genotype H_1H_2, H_1 and H_2 would be strain 1,2. The non-aggressive strain would be strain 0. This system of indicating strain relationships is in direct parallel with the international system

(Black et al,1953) for designating strains of Phytophthora infestans, the fungus causing late blight of potatoes.

SECTION VI.

CURRENT INVESTIGATIONS

1. The prospect of using the resistance of S. multidissectum in the field.

Mr F. G. W. Jones of Rothamsted Experimental Station was supplied with tubers of resistant clones bred from S. multidissectum and is currently testing them against a range of populations of potato root eelworm collected originally with the assistance of the National Advisory Service. This will enable Mr Jones to estimate what percentage of the populations aggressive towards potatoes incorporating the gene H_1 of subsp. andigena could be brought within the scope of control using resistance conferred by the gene H_2 of S. multidissectum.

Dr H. W. Howard of the Cambridge Plant Breeding Institute was also supplied with tubers of the resistant clones. He found (personal communication) that they remained virtually cyst-free after infection by a population which, in selective culture, had become increasingly aggressive towards potatoes of genotype H_1. This result augured well for the usefulness of S. multidissectum in the field.

2. Genetic combination of the resistance of S. multidissectum and subsp. andigena and its application in studying strain relationships.

Potatoes of genotype H_1 and H_2 were crossed. The progeny was replicated by means of cuttings, which were tested against strain 1 (Duddingston strain), strain 2 (Boghall strain) and a mixture of these strains in equal proportions. Clones of genotype H_1H_2 were selected on the basis of freedom from cysts in all three tests.

Selective culture of the strain 1,2 will be attempted, using clones of genotype H_1H_2 as selective hosts for a population already obtained by multiplying a mixture of strains 1 and 2 in a neutral, susceptible host.

It is proposed to use clones of genotype H_1H_2 in determining the incidence of biotypes of strain 1, strain 2 and strain 1,2 in populations resulting from the deliberate mixing and possible mass crossing of strains 1 and 2.

At present, the cross fertility of strains 1 and 2 is questionable, although the chromosome number in both strains is the same ($2n = 18$). The latter information was received (personal communication) from Mr J. Cotton, Zoology Department, King's College, Newcastle upon Tyne, 1.

Even assuming cross fertility, it is still questionable whether the two types of aggressiveness could be combined genetically in a new strain. This would be impossible, for instance, if one type of aggressiveness were recessive to the other.

3. Single matings between biotypes of different strains.

In certain circumstances, this might be the only means of establishing whether crossing was possible.

Single matings were attempted by placing two invasive larvae in each of 100 small pots containing potatoes growing in sterilised sand. Assuming a 1 : 1 sex ratio, 50 matings could be expected, but no cysts were found and probably no females were fertilised. This may have been due to either to cross sterility or/faulty technique, since the chance of a single male's finding a single female under the conditions provided was probably small.

Plate 14. *Solanum infundibuliforme*, resistant to potato root eelworm.

It is proposed to repeat the attempt, using slices of tubers as substrate for the larvae.

4. Extended classification of strain relationships.

Series	Species of potato	Strain reaction Duddingston	Boghall
Tuberosa	S. tuberosum subsp. andigena	+	-
	S. famatinae	+	-
	S. kurtzianum	+	-
	S. microdontum	+	-
	S. gourlayi	±	-
	S. leptophyes	±	-
	S. vernei	-	-
Megistacroloba	S. sanctae-rosae	-	-
	S. raphanifolium	±	+
	S. megistacrolobum	±	+
Tuberosa	S. neohawkesii	±	+
	S. multidissectum	-	+
Cuneolata	S. infundibuliforme	-	+

Level of resistance	sign	strain reaction
above standard	-	nonaggressive
near standard	±	indefinite
below standard	+	aggressive

The strain reactions as indicated above are based on tests of six plants per clone and three clones per species. The results need to be amplified in a few cases and this is being done.

Dr H. Ross, Max-Planck Institute, Cologne and Dr C. A. Huijsman, Stichting voor Plantenveredeling, S.V.P., Wageningen, Holland, are carrying out tests on the same material. Advance information suggests that strains differentiated by each of these workers correspond fairly closely with the Duddingston and Boghall strains in

pathogenicity towards identical clones of the thirteen species listed above.

Progenies of these thirteen species are also being tested jointly, together with progenies of the following species of potato which have never been tested previously for resistance to potato root eelworm.

S. boliviense
S. "camarguense"
S. "carrilloi"
S. chomatophilum
S. herrerae
S. lignicaule
S. liriunianum
S. marinasense
S. "membranaceum"
S. "rockefelleriae"
S. tacnaense
S. species nova

The species in inverted commas are not listed in Hawkes's classification (1956). They were collected by Dr Ross in South America in 1958 and were named provisionally by him.

A plant of each of six clones from each progeny is being tested against each of the Duddingston and Boghall strains. Cysts were beginning to appear on the susceptible controls at the time of writing.

The analysis of the joint results may give further insight into the host/parasite relationship and may provide a basis for international agreement concerning the designation of resistance genes and strains.

APPENDIX:

LIFE HISTORY OF POTATO ROOT EELWORM

Franklin (1951) reviewed the genus Heterodera (Heterodidae, class Nematoda). Fenwick (1959) gave a short, recent account of the genus and Jones (1959) discussed the adaptations to parasitism.

The characteristic feature in the genus is the tough-walled, bladder-shaped cyst which is the form of the fertilised female eelworm at death. The morphology of the cyst, colour, size, presence or absence of a vulval cone and the posterior view, provides the main features used in identifying species. (Cooper, 1955). There are about sixteen species, all parasitic on the roots and underground stems of flowering plants. The host range of H. rostochiensis is restricted to members of Solanaceae. Potatoes and tomatoes are the principal hosts but Solanum nigrum, S. dulcamara, Atropa bella-donna and Hyoscyamus niger, of which only S. nigrum is a weed of cultivation, may act as poor hosts for some populations of the eelworm.

The fully grown cyst of H. rostochiensis is chestnut brown in colour, somewhat shiny, with only one prominent posterior orifice or fenestra (Cooper, 1955) and is spherical in shape, apart from the protruberant neck and head, which remain embedded in the host until the root system decays. Cysts in the mass are superficially reminiscent of turnip seed, although of considerably smaller diameter (————————). The cyst is the persistent

stage in the life-cycle and may contain up to 600 eggs, highly sensitive to a hatching factor emanating from host root systems. The invasive or second stage larvae which emerge from the cyst through neck and fenestra have already shed their first cuticle whilst in the egg. They are colourless worms, barely visible to the naked eye, sluggish in movement, anatomically simple, and/undifferentiated as to sex, possessing a retractable stylet or mouth spear, through which they imbibe the fluid contents of the host plant's tissues. They penetrate to the stele and come to occupy a position marked by a group of multinucleate "giant cells" formed by several cells of the host coalescing. Four moults take place within the root over a period of about six weeks, after which time the sexes are distinct and mature. The female is pyriform, white and opaque, with posterior protruding through a split in the cortex of the root. The colourless, worm-like male eventually lies exposed at the root surface, coiled up within several layers of cast-off cuticle, appearing no more than an opaque, elongate speck on the root to the naked eye. When free, the male moves through the soil, fertilising the sedentary females, which then enlarge rapidly and change colour through yellow to pale orange as the ovaries grow and eggs are laid down. The females are filled with embryonated eggs three or four weeks after fertilisation and become typical cysts after death.

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