A STUDY OF VARIABILITY IN FIELD POPULATIONS OF POTATO CYST NEMATODE (*HETERODERA ROSTOCHIENSIS* WOLLENWEBER) IN RELATION TO RESISTANT POTATOES.

THESIS

submitted by

ANOOP S. BEDI, M.Sc. Agric., Edinburgh.

Candidate for the degree of Ph.D. in the

FACULTY OF SCIENCE, UNIVERSITY OF EDINBURGH,

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SUMMARY

Fifteen field populations of Heterodera rostochiensis Woll., were studied. The distribution of cysts within fields was mapped. Foci of infestation were evident, suggesting that some more or less isolated patches of infestation had probably been initiated by the progeny of a single cyst.

H. rostochiensis varies in pathogenicity towards potatoes incorporating pathotype-specific resistance-genes derived from South American potatoes. Therefore, founder effects within fields could lead to the formation of subpopulations which differed in pathogenicity.

Unpublished results presented as appendix to the thesis had already established a working hypothesis, namely that pathotype A was genetically VaVa or Vavb and that pathotype B was genetically vbvb. There was also some evidence that pathotype B was less fit than pathotype A in mixtures regenerated on fully susceptible potatoes. Together, these facts held out a possibility that a state of balanced polymorphism, promoted by allelism combined with heterozygous advantage, existed in H. rostochiensis.

The genetic constitution of each field population was investigated following the establishment of inbred lines. Each line was initiated by sibmating within the progeny of a single cyst, each parent cyst having been collected at a different site in the field. A second inbred generation was produced similarly; then each line was tested against six differentially resistant test plants. Sister cysts were used singly to supply the inoculum.

It was concluded that the resistance gene (H1) of subsp. andigena and the resistance gene of S. spegazzinii were probably identical by descent, and that the genes (H2) of S. multidissectum and S. sanctae-rosae were also probably identical by descent.

No cysts appeared on H1H2 plants. By definition therefore pathotype E was absent. From this it followed, again by definition that all the cysts formed on H2 plants were pathotype A and all the cysts formed on H1 plants were pathotype B.

Pathotype B was detected in every field but occurred mainly in well isolated patches, suggesting that in other areas it had declined in competition with pathotype A. The mean frequency of pathotype B in the field populations as a whole was found to be 0·017, from which it was calculated that the frequency of the gene vb was 0·13 and that 1 in every 4 or 5 individuals was a heterozygote.

The hypothetical pathotype 0, capable of encysting in neither H1 nor H2 potatoes, was almost certainly not present in any of the populations investigated. All these facts supported the working hypothesis, which precludes the existence of pathotype 0 in its present simple form, and substantiated the view that pathotypes A and B existed in a state of balanced polymorphism.

It was established that the intermediate colour of the cyst was linked with specificity in certain combinations probably governed by super-genes, which are frequently encountered in cases of balanced polymorphism. The significance of balanced polymorphism in parasitic systems is discussed.

VARIABILITY IN FIELD POPULATIONS OF POTATO CYST NEMATODE (*HETERODERA ROSTOCHIENSIS* WOLLENWEBER) WITH RESPECT TO RESISTANT VARIETIES OF POTATO.

GENERAL INTRODUCTION.

It is reasonably certain that potato cyst nematode (*Heterodera rostochiensis* Woll.) must have been introduced into Europe from the Andes of South America, where it ranges at least from Peru (Bazan de Segura, 1952) to North West Argentina (Brucher, 1960; Ross, unpublished), and where many indigenous species of potato, and other members of the nematode's principal host genus, *Solanum*, are to be found. Its European history probably dates from about 100 years ago, according to Jones (1966), in whose estimation it has now spread to more than 80% of the potato-growing land in fields and gardens in Britain.

Details of the life cycle of *H. rostochiensis*, its host range and world distribution are given in Appendix 1.

Solanum tuberosum subsp. *tuberosum*, the "European" potato, lacked resistance to potato cyst nematode until it was hybridised with resistant potatoes: the breeding designed to incorporate this character began some fifteen years ago (Ellenby, 1952; Toxopeus and Huijsman, 1953). Prior to this, there is no evidence that potato cyst nematode was subject to selection in favour of resistance-breaking characters during its dispersion in Europe. The genetic consequences of dispersion in the absence of selection come under the heading of Sewall Wright effect (Wright, 1964)

whereby random changes of gene frequency can occur in small populations over a period of time due to sampling variation between one generation and the next. This also gives rise to the founder effect associated with Mayer (1963), which is extremely important in considering potato cyst nematode, because a single fertilised female or cyst can be solely responsible for the eventual infestation of a whole field. This could lead to extremes of differentiation between field populations, to the extent that a certain gene could be fixed in some populations and absent or in very low frequency in other populations. Such extreme differentiation in respect of resistance-breaking characters was the situation which presented itself following the detection of population-specific resistance genes in all of the species listed in Table 1. The best evidence for this concerns resistance stemming from S.tuberosum subsp. andigena. Jones (1958) and Jones and Pawelska (1963) showed that field populations capable of breaking this resistance had a distinctly regional distribution in England and have also been found to occur throughout Europe (references listed in Table 2).

The similar situation with respect to the resistance of the other species listed in Table 1 is the subject of a paper in course of preparation, (Ross et al., in lit.), which sums up results obtained from the exchange of material between potato breeders in Germany, Britain and the Netherlands over a period of years.

The First Section of the thesis deals with the consequences of dispersion in populations of potato cyst nematode, not between fields, as studied by Jones (1958), but within fields, because it

TABLE 1.

List of host species, with population-specific resistance to *Heterodera rostochiensis*

Solanum tuberosum subsp. *andigena*. Juz. et Buk.	Ellenby	(1952)
" *spegazzinii*. Bitt.	Ross	(1962)
" *juzepezukii*. Buk.	Howard	(1961)
" *multidissectum*. Hawkes.	Dunnett	(1961)
" *kurtzianum*. Bitt. et Wittm.	Huijsman	(1960)
" *sanctae-rosae*. Hawkes.	Dunnett	(1964)
" *verneii*. Bitt. et Wittm.	Huijsman	(1964)
	Rothacker	(1959)
" *megistacrolobum*. Bitt.	Dunnett, Huijsman Ross, (unpublished)	
" *nigrum*	Prummel	(1958)
	Stelter	(1957)

was believed that more or less isolated subpopulations might develop in different parts of the same field during the colonizing phase.

Any resulting variation in the frequency of recessive characters, such as the ability of the nematode to overcome resistance ex subsp. andigena (Jones and Parrott, 1965), could be expected to become more obvious as a result of inbreeding. The Second Section therefore deals with the production of a large number of inbred lines of the potato cyst nematode, each originating in a single fertilised female. Certain difficulties encountered in maintaining single cyst lines are discussed.

The Third Section deals with genetic variation between single cyst lines, which was studied in relation to population-specific resistance genes stemming from (a) subsp. andigena and S. spegazzinii, (b) S. multidissectum and S. sanctae-rosae, and certain combinations of these genes. The position at the outset of this study was that the resistance genes of group (a) were clearly different from those of group (b) but within each group the resistance genes appeared to be indistinguishable, despite their origin in different species of potato. Therefore, it was of interest to try to differentiate further between the genes in each pair of species, or failing that, to try to produce evidence which would tend to show that the genes of a pair were probably identical by descent.

The Third Section also deals with the maintenance of genetic variability in populations of potato cyst nematode, which is discussed with particular reference to the possible existence of a state of balanced polymorphism, a genetic mechanism favouring

heterozygosity, as postulated by Dunnett and Bedi (Appendix 2).

The Fourth Section deals with the relationship between cyst chromogenesis and specificity in potato cyst nematode, an investigation prompted by Guile's observations (1966). This held out the possibility that together with balanced polymorphism of specificity there could be balanced polymorphism of cyst colour, involving a super-gene, since Guile has established that these characters were closely linked. The classic cases of balanced polymorphism, including among others the colour-banding of snail shells, mimicry in insects and sickle-cell anaemia in humans, have been reviewed by Ford (1965). Following this, Person (1966) pointed out the possible significance of genetic polymorphism in parasitic systems.

Broadly speaking, the thesis is that the process of dispersal tends to reduce variability within discrete populations of potato cyst nematode and that genetic flexibility is restored by a system ~~of~~ favouring balanced polymorphism, which may help to explain the difficulties of controlling the parasite by means of varietal resistance in potatoes.

TABLE 2.

The occurrence of resistance-breaking pathotypes of *Heterodera rostochiensis*.

Potato cyst nematode populations overcoming ex. subsp. *andigena* resistance.		
Country	Reference	
Peru	Quevedo, Simon and Toxopeus	(1956)
	Van der Laan and Huijsman	(1957)
Scotland	Dunnett	(1957)
England	Jones	(1957 & 58)
	Howard	(1959)
Federal Republic of Germany	Goffart	(1957)
The Netherlands	Huijsman	(1957)
	Kort	(1962)
D.D.R.	Schick and Stelter	(1959)
	Stelter	(1963)
Belgium	Gooris and d'Herds	(1962)
U.S.S.R.	Kameraz	(1963)
Switzerland	Muster	(1959)
Norway	Roer	(1961)
Greece	Pasehaaki Kountzi, N. *et al.*	(1964)
Poland	Jones and Pawleska	(1963)
Northern Ireland	Jones and Pawleska	(1963)
Channel Islands	Jones and Pawleska	(1963)
Southern Ireland	Anon.	(1966)

SECTION I

POPULATION DENSITY: THE PATTERNS OF INFESTATION IN THE FIELD

POPULATION DENSITY: THE PATTERN OF INFESTATION IN THE FIELD.

Introduction

The potato fields which were selected for the study of the structure of cyst nematode populations were situated in the traditional war-e potato growing districts of South East Scotland, the Lothians and Fife. It was known from the records of the East of Scotland College of Agriculture Advisory Service (made accessible through the kind offices of the Advisory Entomologist, Mr. E. Dunn) that many of the fields in these areas were to some extent infested with potato cyst nematode. In addition, the records provided a case history of each infested field, including details of previous cropping and average population density in terms of cysts etc. Moreover, there was some evidence that potato fields south of the River Forth harboured biotypes capable of encysting in resistant varieties bred from Solanum tuberosum subsp. andigena (Dunnett, 1960a). The close proximity of these fields to the Scottish Plant Breeding Station was convenient in view of the large volume of infested soil which had to be collected and transported as a result of intensive sampling.

It was estimated from a consideration of the labour requirement that not more than about fifteen potato fields could be investigated intensively, envisaging about five soil samples per acre, the production of the same number of inbred lines, and the testing of these lines against seven genotypes of potato. The selection of the fields was guided by two criteria, (a) the age

of the most recent generation of cysts and (b) the distribution of cysts in the field.

(a) This depended on the date of the last potato crop, which was available from the Advisory records.

Since the intention was to establish single cyst lines it was clearly important that cysts with a full complement of viable eggs should be available. Therefore, fields which had not supported potatoes in the two years immediately preceding the start of the investigation (1963-64) were excluded.

(b) It was desirable that viable cysts should be obtainable over the whole area of the field, since it was proposed that the single cysts founding lines should come from sites at spaced intervals. A very patchy distribution of cysts would therefore have limited the numbers of lines which could be established.

Twenty-five fields which met requirement (a) were selected for preliminary sampling (Fig. 1.1) with a view to selecting those which also met requirement (b).

Preliminary sampling

Each field was divided into four to eight equal parts, according to its size. Four to eight samples of soil were taken at intervals from each part of a field and were pooled together to make a composite sample of about 2,000 gms. The number of cysts per gm. of soil in each part of a field was established by washing a well mixed soil sample of known weight in a Fenwick can (Goodey, 1963). The number of cysts extracted are recorded in Table 1.1.

FIG.1.1.

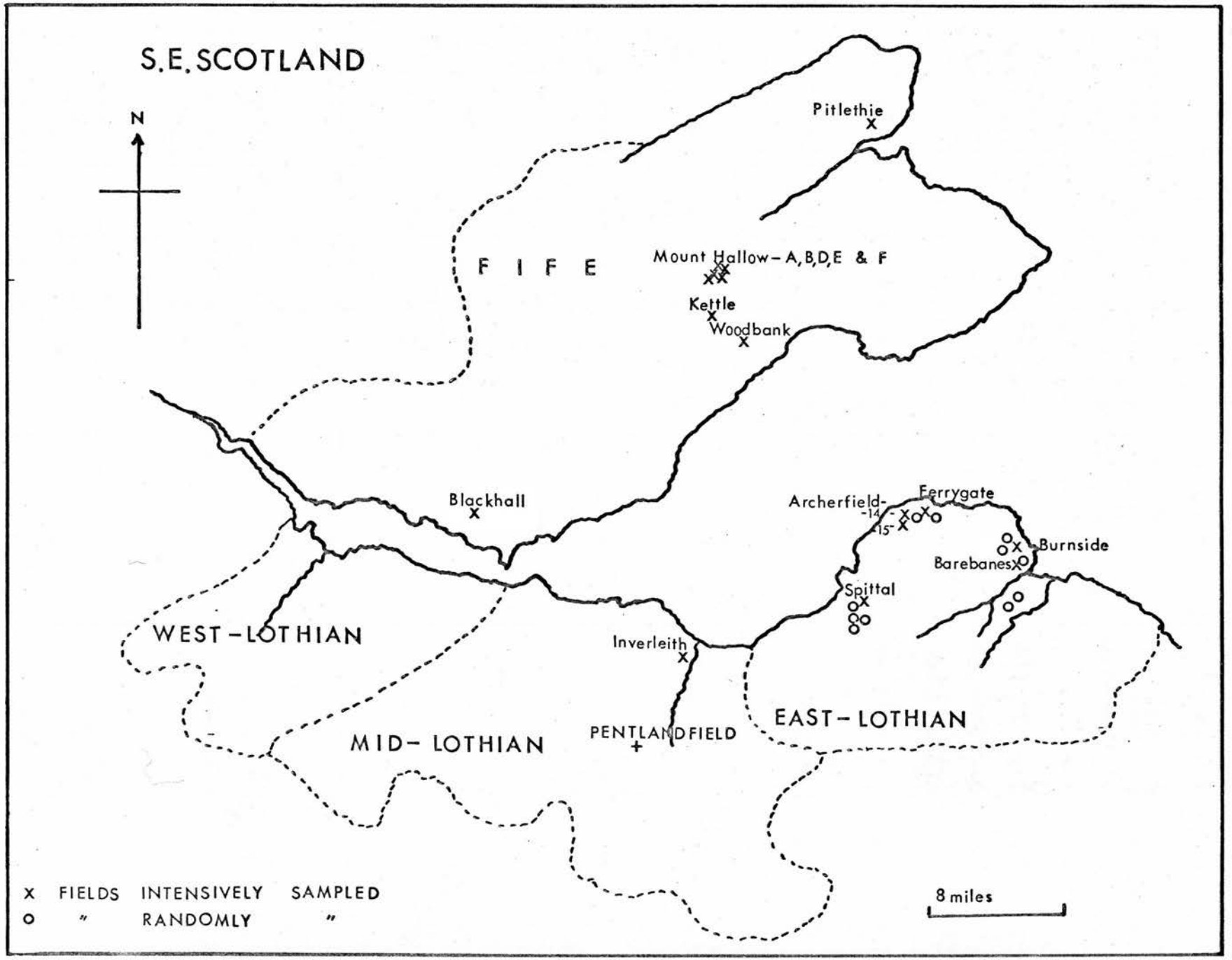

S.E. SCOTLAND
N
Pitlethie
FIFE
Mount Hallow – A, B, D, E & F
Kettle
Woodbank
Blackhall
Archerfield-
Ferrygate
Burnside
Barebanes
Spittal
WEST – LOTHIAN
Inverleith
PENTLANDFIELD
EAST – LOTHIAN
MID – LOTHIAN
X FIELDS INTENSIVELY SAMPLED
O " RANDOMLY "
8 miles

TABLE 1.1

Results of the preliminary sampling of potato fields which had supported a potato crop in 1963 or 1964.

County	Field or O.S. No.	Acreage	Field Division	Cysts/gm soil	Sample weight washed
East Lothian	Ardmore	9	1	0·035	200 gms.
			2	0·015	" "
			3	0·020	" "
			4	0·000	" "
"	Cottage Field	18·8	1	0·011	300 "
			2	0·000	" "
			3	0·003	" "
			4	0·006	" "
			5	0·001	" "
			6	0·000	" "
"	Burnside *	28·17	1	0·066	" "
			2	0·046	" "
			3	0·023	" "
			4	0·023	" "
			5	0·042	" "
			6	0·065	" "
"	Cockedhat	39·7	1	0·040	" "
			2	0·076	" "
			3	0·033	" "
			4	0·023	" "
			5	0·003	" "
			6	0·026	" "
			7	0·006	" "
			8	0·000	" "
"	Barnyard	11·0	1	0·040	" "
			2	0·013	" "
			3	0·000	" "
			4	0·000	" "
"	Barebanes*	14·61	1	0·040	" "
			2	0·140	" "
			3	0·045	" "
			4	0·020	" "
"	Spittal 8	12·0	1	0·010	" "
			2	1·290	" "
			3	0·003	" "
			4	0·000	" "
"	Spittal 9*	34·0	1	0·873	" "
			2	1·196	" "
			3	1·236	" "
			4	0·546	" "
			5	0·160	" "

TABLE 1.1 (Contd.)

County	Field or O.S. No.	Acreage	Field Division	Cysts/gm soil	Sample weight washed
			6	0·110	300 gms.
			7	0·103	" "
			8	0·070	" "
East Lothian	Spittal 10	12·0	1	0·006	" "
			2	0·023	" "
			3	0·000	" "
			4	0·003	" "
"	Spittal 11	18·0	1	0·006	" "
			2	0·000	" "
			3	0·000	" "
			4	0·000	" "
"	Spittal 12	15·0	1	0·001	" "
			2	0·000	" "
			3	0·000	" "
			4	0·000	" "
			5	0·000	" "
			6	0·000	" "
"	Archerfield 13	18·0	1	0·193	" "
			2	0·001	" "
			3	0·001	" "
			4	0·743	" "
			5	0·010	" "
			6	0·000	" "
"	Archerfield 14*	12·78	1	0·293	" "
			2	0·106	" "
			3	0·403	" "
			4	0·036	" "
"	Archerfield 15*	20·25	1	0·056	" "
			2	0·596	" "
			3	0·506	" "
			4	0·050	" "
"	Ferrygate*	33·58	1	0·140	" "
			2	0·033	" "
			3	0·580	" "
			4	0·416	" "
			5	0·025	" "
			6	0·060	" "
"	Ferrygate 17	28·0	1	0·416	" "
			2	0·030	" "
			3	0·006	" "
			4	0·013	" "
			5	0·000	" "
			6	0·020	" "

Table 1.1 (Contd.)

County	Field or O.S. No.	Acreage	Field Division	Cysts/gm soil	Sample weight Washed
Fife	Kettle*	8·07	1	0·025	200 gms.
			2	0·025	" "
			3	0·070	" "
			4	0·030	" "
"	Pitlethie*	17·09	1	1·330	" "
			2	1·189	" "
			3	1·440	" "
			4	1·420	" "
"	Woodbank*	12·19	1	0·097	400 "
			2	0·102	" "
			3	0·380	" "
			4	0·507	" "
"	Blackhall*	19·27	1	0·410	" "
			2	0·750	" "
			3	0·280	" "
			4	1·168	" "
			5	0·880	" "
			6	0·300	" "
"	Mount Hallow A*	3·24	1	2·822	" "
			2	3·547	" "
	Mount Hallow B*	1·53	1	1·149	" "
	Mount Hallow D*	2·74	1	2·585	" "
	Mount Hallow E*	2·10	1	2·540	" "
	Mount Hallow F*	3·48	1	2·500	" "

* Fields selected for intensive sampling.

Six fields in East Lothian and nine fields from Fife, those marked by an asterisk in Table 1.1, appeared to meet the requirement (b) and were selected for intensive sampling. Their locations are plotted in Fig. 1.1.

Intensive sampling.

Rate of sampling. The selected potato fields varied in area from 34 acres (Spittal) down to 1·53 acres (Mount Hallow B). The average area was 14·20 acres. Since it was proposed to collect between 80 and 100 soil samples per field, this necessitated about twelve samples per acre from fields smaller than eight acres and about five samples per acre from bigger fields. The samples were taken at the intersections of a grid of squares, at intervals of 30 yards in fields larger than eight acres and 20 yards in smaller fields. Some additional samples were taken near the border or in corners of fields which were irregular in shape. By systematic sampling in this way it was possible to produce maps of population density and also, at a later stage, maps of the distribution of phenotypes or pathotypes.

In all, 1,148 separate soil samples from fifteen potato fields were collected.

Size of sample. Samples of soil to a depth of eight inches and weighing 800 to 1,000 gms. were collected by means of a concave turfing spade which had a blade 11½ inches long, tapering from 5¾ inches to 2 inches at the tip. The samples were kept separately in double-bottomed kraft paper bags lined with grease-proof paper, marked with reference numbers to identify their

points of origin on the field grids.

Treatment of samples. Each soil sample was dried in a metal tray in a fume-cupboard fitted with an exhaust fan, which drew over the samples a gentle current of air at room temperature (65°F). After drying, each sample was sieved to remove stones and other large debris. The soil samples were then stored in their respective paper bags, until required for washing.

Recovery of cysts.

Cysts of all Heterodera species were extracted by flotation from weighed quantities of soil. The use of the normal apparatus for this purpose, the Fenwick can (Goodey, 1963), was, however, found to be too time consuming. All four parts of the apparatus had to be washed clean before the next sample could be put through, in order to avoid any mixing of cysts from different samples. Moreover, the number of cysts recovered was to some extent dependent on the length of washing time, but prolonged washing produced cysts which were somewhat water-logged and did not always float well enough to be trapped on the filter paper in the collecting funnel.

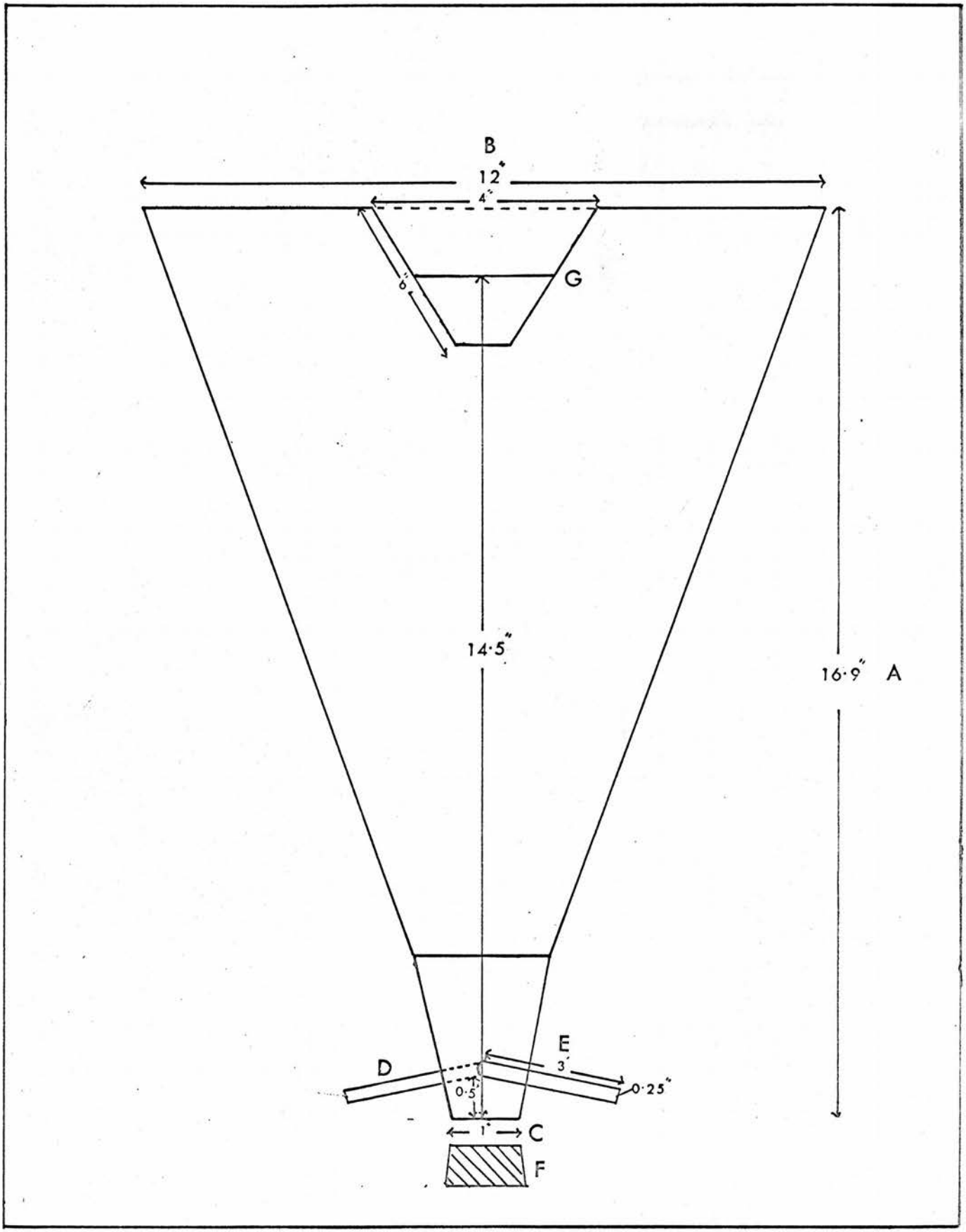
The large volume of soil that had to be washed (200 gms. and more) in order to recover a sufficient quantity of cysts from samples from sparsely infested fields, made impracticable the technique of shaking of the samples in a conical flask partially filled with water (Goodey, 1963). A two-litre conical flask was tried, unsuccessfully.

Eventually, saving in time with no loss of accuracy was achieved by the following new technique, using the apparatus illustrated in Fig. 1.2, consisting of a funnel made out of copper sheet. The neck of the funnel is fitted with two copper inlet tubes, which can be connected to the same water tap through a rubber tubing and a 'T' junction. The inlet tubes are so positioned that the incoming jets of water form a vortex which keeps the soil in the funnel in continuous agitation. Lighter particles are carried upwards as the funnel fills. The force of the water current gradually decreases as the funnel broadens upwards, so that only the lighter debris including cysts reaches the level of the overflow spout.

This makes use of a steady current of water to separate the cysts from the soil and to assist in bringing them to the surface, instead of relying on the natural buoyancy of the cysts as in the conical flask methods. By comparison, also, the Fenwick can suffers from the disadvantage of having the inflow and outflow at nearly the same level, producing two opposing currents causing considerable turbulence which delays the overflow of cysts.

The usefulness of the new apparatus was investigated experimentally, taking into account its optimum time of operation per sample, including samples of different soil types and its efficiency of extraction as compared with the Fenwick can and conical flask methods.

FIG.1.2.



Optimum time of operation. To determine the optimum time of operation, samples weighing 300 gms. were washed for 1, 2, 3, 4 and 5 minutes, respectively. This procedure was repeated three times. The average number of cysts counted per replicate is recorded in Table 1.2. After washing each sample, ~~in~~ the funnel ~~it~~ was emptied through a sieve (60 to 100 mesh), and then the sludge in the sieve was dried and transferred to a conical flask for the recovery of any remaining cysts by flotation.

TABLE 1.2

Percentage recovery of cysts from field samples washed in the apparatus (Fig. 1.2) for various periods

Washing time in minutes	Number of cysts in 300 gm. soil sample*		Percentage recovery
	Whole sample washed in funnel	Sludge dried and washed in conical flask	
1	192	13	93·65
2	197	6	97·07
3	203	2	99·02
4	204	1	99·51
5	205	-	100·00

* Average of three replicates

The washing time required for about 99% cyst recovery appeared to be between three and four minutes for an average field sample.

Optimum time of operation with different soil types. Samples weighing 300 gms. of (a) clay soil, (b) sandy soil, and (c) a potting soil containing sand and peat, were washed for 1½ and 3½ minutes respectively in three replications. The average number of cysts recovered per replicate is recorded in Table 1.3. Any cysts remaining in the funnel were recovered by the method described earlier.

TABLE 1.3

Percentage recovery of cysts from 3 different soil types washed for various periods

Soil type	Washing time in minutes	Number of cysts in 300 gms. soil sample *		Percentage recovery
		Whole sample washed in funnel	Sludge dried and washed in conical flask	
Clay	1½	105	27	79·54
	3½	130	2	98·48
Sand	1½	128	4	96·96
	3½	132	-	100·00
Standard potting compost.	1½	78	54	59·09
	3½	114	13	86·36

* Average of three replicates.

The percentage recovery of cysts varied with type of soil and washing time. With soils containing a high proportion of clay and other organic matter cyst recovery was poor, while in sandy soils cyst recovery was highest. Probably a higher percentage of cyst recovery in organic soils could be achieved

by prolonging the washing, because even water-logged cysts would tend to be carried upwards in the water current.

Comparison of the efficiency of extraction by different methods. The percentage of cyst recovery using the new apparatus was obviously satisfactory. Therefore, the best method for the purpose would be the one requiring the least time of operation. Three batches of twenty-four samples were washed by each of the three methods, viz. conical flask, Fenwick can and the new funnel. The average time required per sample by the different methods is recorded in Table 1.4. This includes the time required for cleaning the apparatus between samples.

It is apparent from the results in Table 1.4 that a significant saving in washing time was achieved by using the funnel. This saving in time was partially due to the ease with which the funnel could be cleaned, by simply removing the drain plug F (Fig. 1.2). Since it was proposed to test single cyst lines in sand culture, using pots holding about 50 to 70 gms. it was estimated that on average 1½ to 2 minutes would suffice for the recovery of cysts from each pot by the new technique.

Results

The majority of the soil samples which were washed contained cysts of *Heterodera* species other than *H. rostochiensis*. Cysts of *H. punctata* were widely distributed but never numerous. These

TABLE 1.4

Time taken for the extraction of cysts by flotation using three types of apparatus

Type of apparatus	Sample size	No. of samples washed	Soil type	Total No. of cysts recovered	No. of cysts/gm. soil	Total washing time	Mean washing time per sample
Conical flask	70 gms.	24	sand	1693	1·003	55 min.	2·29 min.
	" "	24	"	629	0·374	63 "	2·62 "
	" "	24	"	1308	0·779	65 "	2·70 "
Fenwick can	150 gms.	24	sand	2674	0·740	110 "	4·58 "
	400 "	24	clay	4879	0·508	115 "	4·79 "
	200 "	24	sand	1984	0·205	110 "	4·58 "
Funnel	300 "	24	sand	16338	2·269	45 "	1·87 "
	100 "	24	clay	3064	1·276	50 "	2·08 "
	100 "	24	sand	6966	2·902	40 "	1·66 "

cysts could be distinguished superficially from those of H. rostochiensis, by their thinner-walled appearance. It was not possible to examine doubtful round cysts in detail in order to distinguish between H. rostochiensis and H. punctata because of the time required, and in any case this was hardly necessary since the proportion of H. punctata cysts was expected to be negligible. The other species present had lemon-shaped cysts clearly distinct from those of H. rostochiensis. H. avenae appeared to be the most frequent, although some lemon-shaped cysts were finally identified as H. trifolii.

The author is indebted to Dr. Tom Mabbott for assistance in establishing the identity of specimens.

H. rostochiensis cysts of all ages and conditions were counted and stored in 1 ml. polythene tubes, which were kept in darkness at room temperature (65°F) and humidity.

The number of cysts of H. rostochiensis per gm. of soil at each intersection of the field grid was recorded and mapped as "nemagraphs", Maps 1a to 15a. These were produced on the assumption that each record represented an area of 400 to 900 square yards, depending on the size of the field.

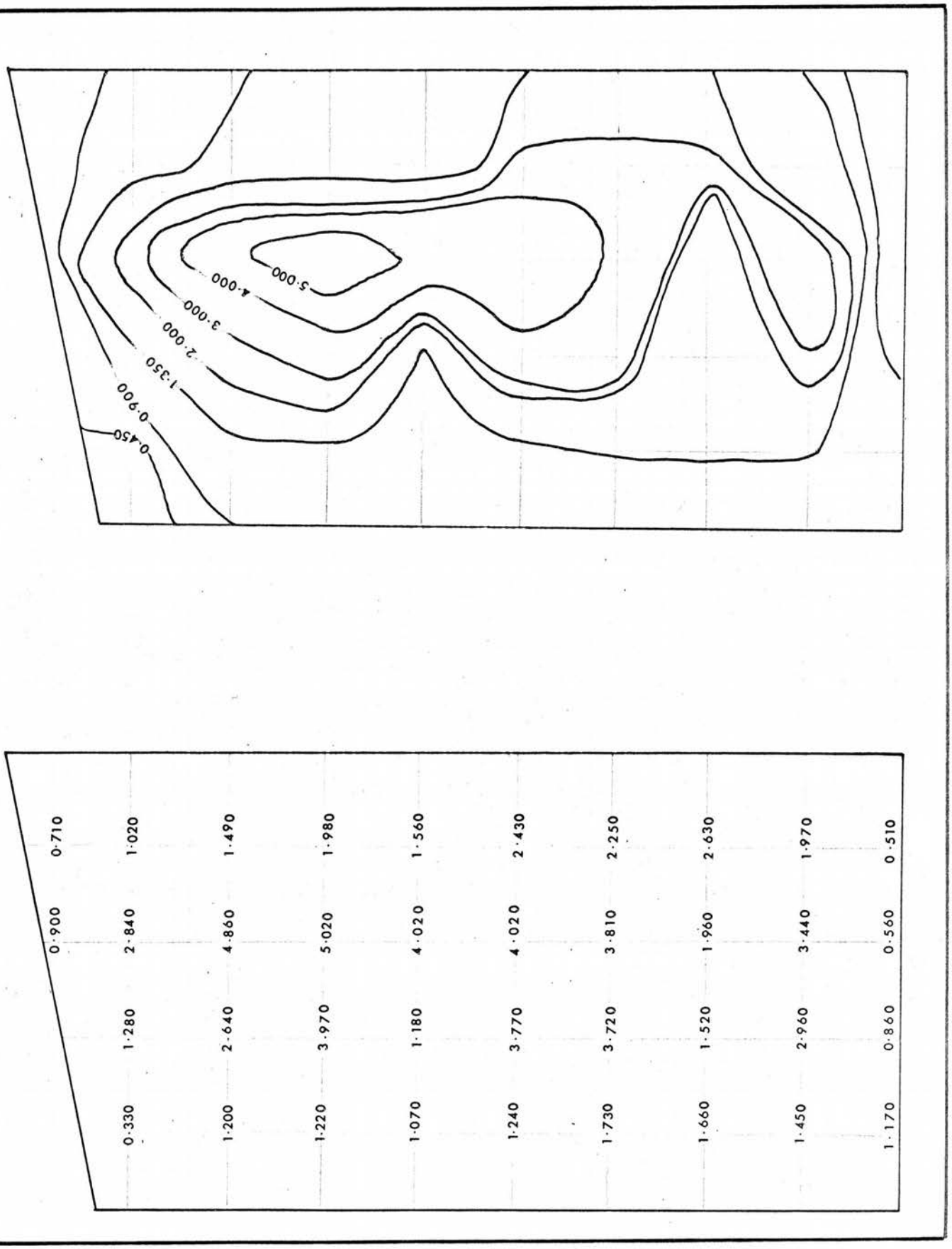
The plotting of nemagraphs

It soon became obvious that the distribution of cysts in most of the intensively sampled fields was very patchy, ranging from cysts absent to a maximum of 10 cysts per gm. in areas where

populations had probably reached a ceiling level. Because of this, subdividing the overall range at equal intervals gave an extremely skewed distribution of samples falling into the different classes, such that most of the samples fell into the lowest class and the rest were clustered at the higher end of the scale. This kind of distribution gave minimal information about the way in which an infestation had probably developed. In order to bring this out better, finer graduations were obviously required at the lower levels of infestation. This raised the problem of deciding the most appropriate size of class interval in relation to the size of sampling error. If the variation in cyst density at the lower end of the scale was mainly the result of sampling error, a mosaic pattern would emerge. On the other hand, if a coherent pattern emerged, then sampling error was not important. This was the guiding principle in the production of the nemagraphs.

It was found that if the overall ranges in cyst numbers were subdivided into four equal parts above and below the mean, coherent and informative patterns emerged. In many potato fields where the mean was nearer the lower end of the scale, the intervals below the mean were now much narrower than the four equal intervals above the mean. In the extreme case (Map 9.a) the ratio was 1:16. Adjusting the class intervals in this way helped to focus attention on variation in the more lightly infested areas, those areas in which infestations were still increasing and spreading, and where continuous gradients of density might be expected.

FIG. 1.3.


0·450
0·900
1·350
2·000
3·000
4·000
5·000
0·710
1·020
1·490
1·980
1·560
2·430
2·250
2·630
1·970
0·510
0·900
1·280
2·840
4·860
5·020
4·020
4·020
3·810
1·960
3·440
0·560
0·330
1·200
1·220
1·070
1·240
1·730
1·660
1·450
1·170
0·860

Draughting of nemagraphs

The squared sampling grids were superimposed on the field maps, which were made to an appropriate scale within the range of 10 - 30 yards to 1 cm. At each intersection of the grid, the number of cysts per gram of sample was recorded. The distances between each sampling point and the next along the grid in every direction were subdivided at points corresponding to the class limits, assuming a uniform gradient between neighbouring sampling points. Then the positions of corresponding class limits were joined freehand by lines called isopleths, as illustrated in Fig. 1.3.

Finally, the isopleth maps were made coropleth maps, by a mapping technique which will be obvious from Maps 1a to 15a. This had an advantage of making variation in population density immediately obvious to the eye. One refinement was to indicate by means of sparse dotting that the areas yielding cyst-free samples were not necessarily cyst-free, but probably harboured cysts which were too few to be detected by soil sampling at the rate of one sample every 400 or 900 sq. yards. In order to obtain cysts from such areas either the sample size had to be increased or the sampling area reduced. Jones (1955) calculated that there was more than a 5% probability of recovering no cysts from a 100 gm. sample collected from a field having a population between 30 - 60 x 10^6 eelworms per acre.

Presentation of nemagraphs

Fifteen nemagraphs are figured (Maps 1a to 15a), each representing a particular field. A short description of each field and details of its previous cropping history are given on the page facing the corresponding nemagraph.

Discussion

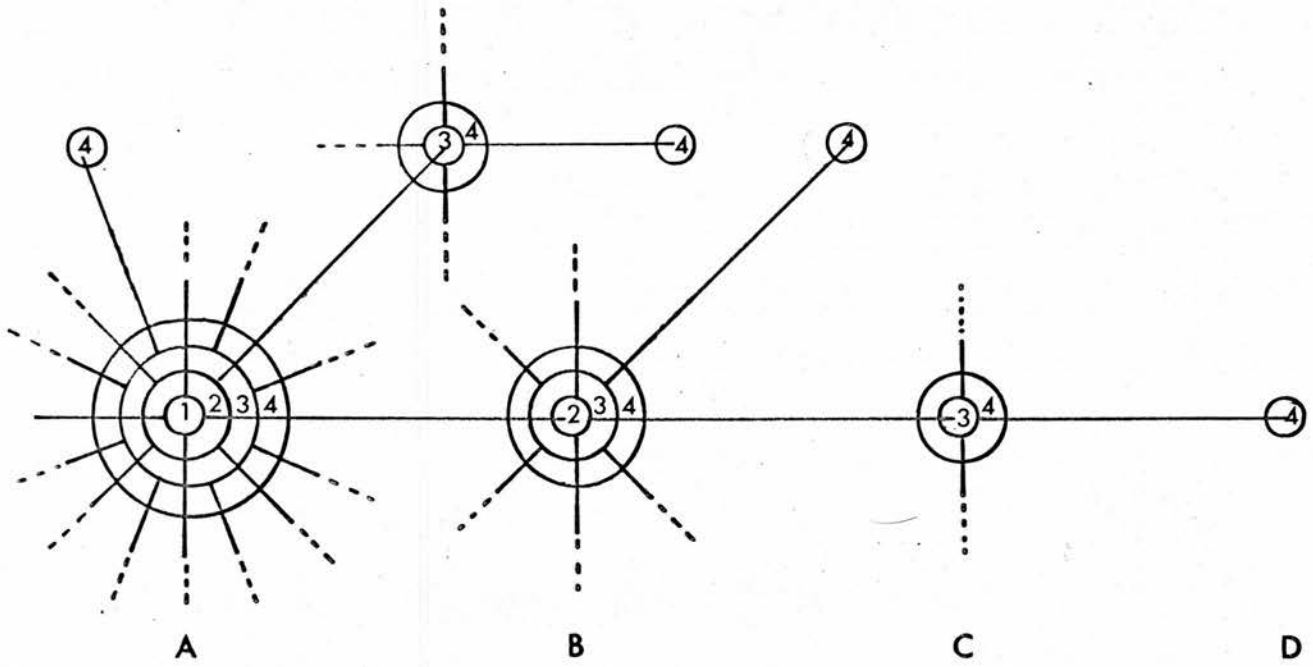
The work of Wallace (1960) and Peters (1953) suggests that the invasive larvae of Heterodera rostochiensis migrate no more than a few centimetres from the parent cyst. Moreover, this migration must be very largely restricted to the periods when potato crops are growing because hatching is minimal in the absence of the hatching factor which diffuses from potato roots. Therefore, while this migration or active spread can be assumed to occur laterally in all directions when potatoes are grown, it can account for no more than a very small periodic extension of infested patches in the field.

Passive spread of the potato cyst nematode, brought about by the transference of cysts with viable contents from place to place by agencies such as agricultural implements, the feet of animals, wind, and surface water, is certainly much more important in the field. Such passive spread is not, of course, restricted to the periods in which potatoes are growing but occurs throughout the year and every year. It is unlikely to occur evenly in all lateral directions, because many agricultural operations, beginning with ploughing, are done in a certain direction determined by the

shape and topography of the field. In addition, surface drainage is influenced by the lie of the land and the direction of the ridges put up for row crops. The prevailing direction of the winds may be important, too, in the case of light sandy soils. Effects of these factors on passive spread are discussed in specific instances in the notes facing each nemagraph.

Before studying the nemagraphs, it is important to differentiate between the concepts of continuous and discontinuous spread or dispersal of potato cyst nematode. Continuous spread results from a combination of active spread with passive spread due to earth moving operations, and gradually increases the area of infested patches. Discontinuous spread occurs when cysts are carried in any way beyond the limits of continuous spread and initiates new patches of infestation. This means that fields will tend to have isolated centres of infestation, a primary focus or several contemporary primary foci, secondary foci, and so on, each surrounded by a zone of continuous spread. This process is illustrated diagrammatically in Fig. 1.4, by letters indicating the sequence of new patches being formed and serial numbers indicating the periodic extensions of established patches. Since potatoes are not normally grown year after year in the same field, each serially numbered zone is the infested area resulting from cumulative spread under a cycle of crops, which ends in spread and multiplication under a potato crop. In this year of multiplication contemporary new foci would be established from cysts isolated at any time since the previous potato crop.

FIG.1.4.



Continuous spread

1 st. Year of spread.
2 nd. " " "
3 rd. " " "
4 th. " " "

Discontinuous spread

A Primary focus.
B Secondary "
C Tertiary "
D Quaternary "

Bannister (1965) explained the spread of Pinus radiata in New Zealand in terms of continuous and discontinuous spread; he had the advantage of being able to find the ages of trees by counting annual rings.

The extent to which the patterns of infestations can be explained in this way is considered briefly in relation to each nemagraph in the notes on the facing pages.

With these points in mind the nemagraphs can now be examined in more detail, for any clues to the probable origin, development and age of the infestations which they portray.

Many of the populations which were mapped appeared to have a single primary focus of infestation, such as could be attributed with a high degree of certainty to a single immigrant cyst; if a group of founder cysts were involved, it is likely that they would have been scattered to some extent, and so have given rise to separate, contemporary primary foci.

The frequency of cysts at the centres of maximum infestation in the fields which were studied ranged from 84 to 1000 per 100 grams sample of soil. To put this into perspective, it has been calculated by Jones (1955) that a founder cyst given tenfold multiplication for six generations, requiring six potato crops within a period of up to 30 years, would produce a small area at the centre of infestation where the probability of detecting a single cyst in a 100 gram sample would be only 0·6.

The question of the age of infestations can be approached directly, from measurements of the mean radius of continuous

spread surrounding a primary focus.

It is suggested that continuous spread is unlikely to exceed six feet in a year, which is roughly the distance over which soil is scattered by a potato spinner. Annual spread would probably be less if potatoes were not grown every year, because a potato spinner spreads soil further than most implements.

The zones of continuous spread surrounding one primary focus (Map 3a) extended to over 200 yards: even allowing for the suggested maximum spread of six feet per year, the age of this infestation works out at 100 years. On the same basis, the infestations in general appeared to be from 35 to 100 years old.

These estimates may need to be revised when more information on the rate of continuous spread becomes available but meantime they agree remarkably well with the suggestion by Jones (1966) that potato cyst nematode was introduced into Europe about 100 years ago. It was first detected in Scotland 55 years ago, in 1913 (Massee, 1913) by which time many fields, including, most of the fields featuring in this investigation, were undoubtedly infested to some extent. Such fields were infested, therefore, in the early colonizing phase of the eelworm in Scotland, when it may be supposed that few populations were high enough to attract attention by producing symptoms in the potato crops, and when the scale of transmission of cysts from one field to another on seed tubers or by any other means would be minimal.

The prevalence of secondary and later centres of infestation in nearly all of the fields, with an inexplicable exception in

Mount Hallow F (Map 15a), must be attributed mainly to discontinuous spread within fields because this must be considered certain to occur from the beginning of an infestation, whereas secondary immigration from outside is conjectural.

The implications of discontinuous spread within segregating populations and secondary immigration from outside are the same; in either event founder effect opens up a possibility of genetic differentiation between more or less isolated subpopulations within the same field. The way in which this was investigated is explained in the following Section of the thesis.

SECTION II

THE PRODUCTION AND MAINTENANCE OF SINGLE-CYST INBRED LINES OF POTATO CYST NEMATODE ON ORDINARY COMMERCIAL VARIETIES

THE PRODUCTION AND MAINTENANCE OF SINGLE-CYST LINES OF POTATO CYST NEMATODE ON ORDINARY COMMERCIAL POTATO VARIETIES.

Introduction.

The literature on the inheritance, permanence and scope of resistance to potato cyst nematode relates almost wholly to sample populations which were contained as eggs in multiple-cyst inoculum at the start of investigations, e.g. by Dunnett (1957); Jones (1957); Howard (1959)a; Goffart (1960); Huijsman (1963) and Jones and Pawleska (1963). In measuring resistance, there can be no objection to multiple-cyst inoculum, provided that the corresponding resistance-breaking character is absent or occurs in very low frequency in the population which is used. Difficulties arise when this is uncertain.

Firstly, a low yield of cysts, indicating a degree of resistance to a population as a whole, could be due to complete resistance to one part of the population coupled with no resistance to a second distinct or segregating fraction within the population. To complicate matters further, there need not even be a clear-cut, monofactorial difference between the resistance-breakers and the rest of a population; there could be a more or less continuous range in the degree of adaptation of individual biotypes, governed by a gene complex.

Secondly, if distinct pathotypes exist, are they fully interfertile and nonselective in mating?

Thirdly, in estimating the frequency of resistance-breaking biotypes by Jones' method (1957, 1958), which is to express the number of cysts found on resistant test plants as a percentage of those formed on susceptible test plants, there is a possibility of bias due to the 'built in' assumption that all classes of biotypes compete to the same extent in both the resistant and susceptible test plants. This would seem to be doubtful in view of the fact that the biotypes which are incapable of breaking resistance soon cease to develop in resistant plants.

The investigation of the separate progenies of single cysts offers a new approach to problems of population structure, although this kind of work has special problems of its own. It has the additional advantage that close inbreeding can be maintained by selecting a single cyst from the progeny of a single cyst and so on for generations of brother-sister matings. Inbreeding brings out recessive characters and, if continued, leads to fixation at more and more loci, some characteristics becoming fixed while others are lost in a line. Unfortunately, multiple mating has been demonstrated in potato cyst nematode, so that the severity of inbreeding could be reduced by more than one brother fertilising the same female in any generation. Moreover, Li (1955) has shown that in theory many brother-sister matings, excluding multiple fertilisation, are required to ensure homozygosity at the locus of a particular pair of alleles, although a high probability of fixation (·601) is obtained after 7 generations. Such extended inbreeding was obviously beyond the scope of this thesis, and only two inbred generations could be produced in the time available.

The first inbred generation was produced from cysts selected from the batches collected at each grid intersection in the fields. A cyst from each batch was placed in a pot with the potato variety Craigs Defiance. From each of the single-cyst lines thus established, a single cyst was selected to produce a second inbred generation on Craigs Defiance.

The sampling involved in the formation of the inbred lines was genetically random, in that they were produced on potatoes lacking all resistance genes. It follows that any dispersion of gene frequencies between the lines could not be accompanied by changes of gene frequency in the population of lines as a whole. In this connection Falconer (1961) stated, "the lines come to differ in gene frequency, though the mean in the population as a whole remains unchanged". The gene frequency of the base or parent population could be restored, or obtained, if all the lines representing it were bulked, or were considered as a whole, at any corresponding stage of their parallel development. This principle was the basis for the calculation of gene frequencies in the following Section of the thesis.

Materials

Single cysts were selected from each of 1,085 samples of cysts, corresponding to the number of grid intersections at which at least one cyst was found in fifteen fields. The tubers of Craigs Defiance used throughout were drawn from virus-tested stocks to exclude the possibility of poor growth and development due to virus infection.

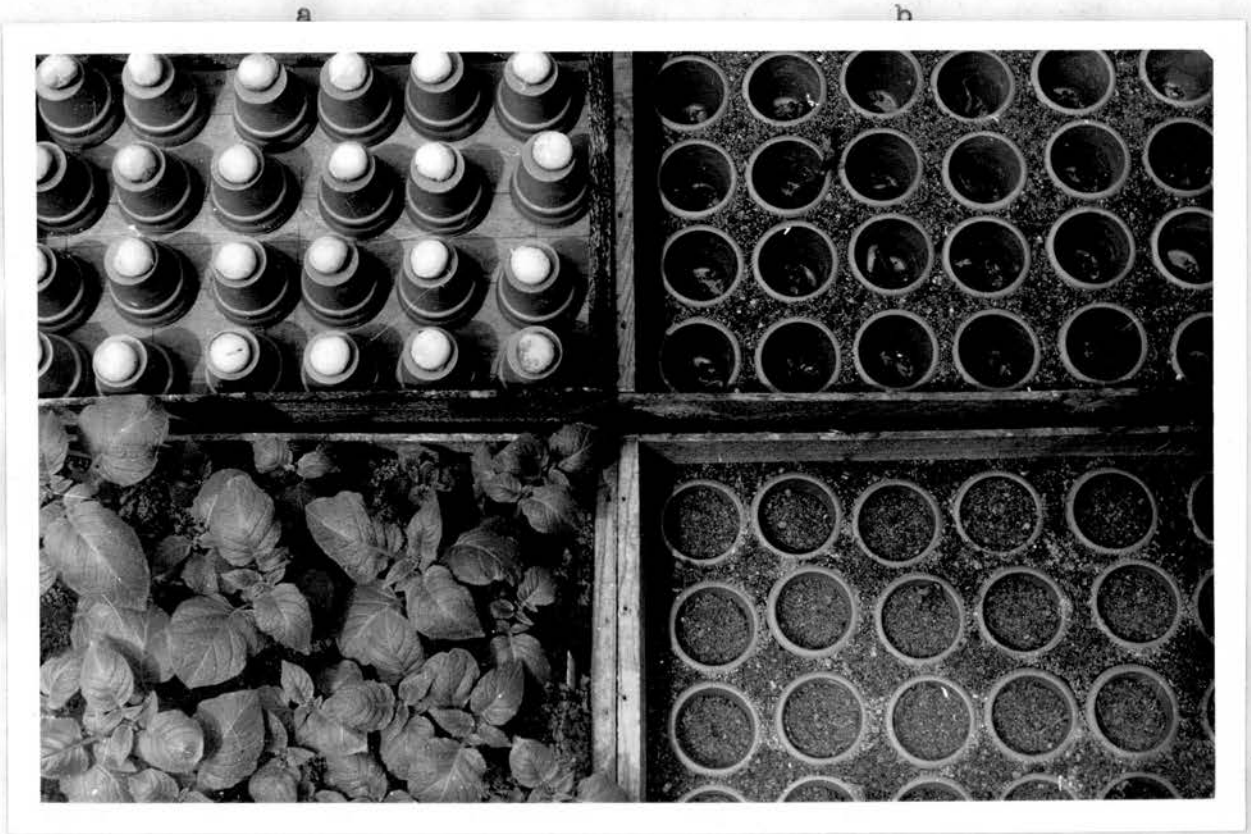
Single-cyst technique

The plants were grown up through the drainage holes of very small clay pots, of the nominal two inch size, which were embedded in soil in wooden fish boxes measuring 14¾" x 9" x 4½". The accompanying photograph (Fig. 2.1) shows how this was done. The frame of a wooden box was fitted over a wooden platform 1¼ inches high, on which 24 pots were then placed upside down leaving the same distance (1¼ inches) above and below the pots within the frame. Potting soil was packed between the pots and up to the level of the bottoms of the pots. Hemispherical seed pieces, excised by a melon scoop, were set in place with the sprouts in a position to grow through the drainage hole. The seed pieces were covered with potting soil to the level of the frame and a wooden cover was screwed in position. This became the base of the box when the box with the wooden platform still in place was turned over. The platform was then removed. The pots contained no soil at this stage, because any soil that had entered through the drainage holes in the packing process had been allowed to escape through holes in the platform. The pots were then partially filled with washed sand containing John Innes base fertiliser at the rate of 4 oz. per bushel. A single cyst was positioned on the inner wall of each pot by means of a fine camel hair brush, and sand was added until the boxes were filled. This covered the pots with 1¼ inches of sand. Each pot held between 70 to 90 gms. of air dry sand.

The full boxes were placed in concrete troughs on a layer of

sand covering soil heating cables, which ran in the grooves of corrugated asbestos sheets. The temperature in the boxes was maintained thermostatically at 68°F ± 5 through the growing season. Water could drain away quickly beneath the corrugated sheets.

a b



d c

Fig. 2.1 (a) Pots and seed pieces in position prior to packing the box with soil. In practice, soil was packed between the pots before the seed pieces were set in place.

(b) Box right side up, with sprouts peeping through the drainage holes.

(c) Pots inoculated with single cysts and partially filled with sand and fertiliser mixture.

(d) The plants two to three weeks after inoculation.

This method of single-cyst culture had several advantages:-

(1) The plants grew strongly and uniformly, because their roots had a free run in good potting soil between and below the pots.

(2) A shoot growing through a drainage hole effectively blocked it and helped to prevent any cross infection by preventing larvae from escaping in drainage water. This meant that the plants had to be irrigated, which was done at weekly intervals, by raising the water table in the trough to the level of the bottomsof the pots.

(3) Confining the small progenies of single cysts within small pots was possibly beneficial to the extent that it maintained population density at a level consistent with an adequate frequency of mating.

(4) Since the surface area of the pot-balls was large in relation to their volume, the correlation between the numbers of cysts visible on the root-mat and the total present was probably better than in larger pots.

(5) The results could not be affected by roots spreading from one pot to another within a box, because each box contained test plants of one genotype only.

(6) Only a small quantity of sand had to be washed in order to recover all the cysts in a pot. The sand contained little or no organic debris, which facilitated the extraction and counting of cysts.

(7) The technique was space and labour saving. The boxes could be stacked up and left to dry out until it was convenient to deal with the pot contents.

The glasshouse which was available contained two concrete troughs, each capable of holding 65 boxes or a crop of up to 1,560 plants at a time. By staggering the dates of planting (Table 2.4) in the two troughs it was possible to grow up to seven such crops in the greenhouse in a year. Supplementary lighting was supplied by mercury vapour lamps for up to twelve hours daily from December to February. Each crop remained in position until the cysts were becoming cream or pale lemon in colour, when the plants were cut down, and the boxes were set aside. As soon as possible thereafter the pot contents were emptied into paper bags and left to dry off.

Presentation of results

The yield of cysts produced by sib mating in single-cyst lines over two generations on Craigs Defiance are entered in the Field Maps 1b to 15b. At any point on a map, a black figure records the number of cysts produced by the progeny of a single cyst collected at that point in the field. The corresponding red figure is the number of cysts produced from one of her daughter cysts.

The mean yields of cysts and coefficients of variation for the two generations of the single-cyst lines representing the different fields are set out in Table 2.1.

Analysis of results

The mean coefficient of variation in cyst production was

TABLE 2.1

The mean yield of cysts and coefficients of variation for two generations of the single-cyst lines representing different fields

Field Population	Total No. of single-cyst lines			Percentage of single-cyst lines reproducing		Mean yield of cysts		Standard deviation		Coefficient of variation	
	P	S1	S2	S1	S2	S1	S2	S1	S2	S1	S2
Burnside	127	127	74	58·2	97·3	5·2	13·3	22·4	26·6	243·0	101·9
Barebanes	63	63	46	73·0	71·7	18·5	22·0	7·9	23·7	42·7	10·7
Spittal	160	160	118	78·1	96·9	30·6	26·3	56·1	25·3	54·4	78·7
Archerfield 14	53	49	35	67·9	100·0	48·1	46·5	43·1	30·1	89·5	63·8
Archerfield 15	70	70	69	98·5	100·0	101·0	72·7	65·7	41·9	65·0	55·9
Ferrygate	119	119	92	73·9	90·6	3·8	23·0	8·4	36·8	215·0	130·0
Kettle	45	45	41	91·1	94·5	7·3	33·1	7·6	24·3	104·0	66·2
Pitlethie	97	97	96	98·9	93·6	46·9	10·3	41·2	14·4	87·8	139·8
Woodbank	54	54	48	84·7	87·7	23·0	10·2	20·5	9·1	89·1	89·2
Blackhall	129	129	121	92·2	84·1	30·1	7·7	10·8	9·4	35·8	120·5
Mount Hallow A	44	44	42	95·4	80·4	21·0	12·1	27·6	14·7	131·4	121·0
Mount Hallow B	19	19	18	94·7	66·6	13·5	6·0	18·1	8·9	134·0	148·0
Mount Hallow D	36	36	36	100·0	77·7	31·2	8·8	32·2	8·5	102·8	95·5
Mount Hallow E	26	26	26	96·1	88·7	22·4	13·1	20·4	16·6	91·0	126·7
Mount Hallow F	38	38	35	92·1	78·7	22·6	7·4	26·2	9·4	115·9	125·0
Means				80·18	81·98	28·3	20·8	27·2	19·9	106·7	97·53

P = Parent cysts collected from the field in 1964 and 1965.

S1 = First inbred generation, 1965.

S2 = Second inbred generation, 1966.

106·7% in the first generation of the single cyst lines, and 97·5% in the second generation. This extreme variation probably resulted from a variety of causes, of which the following had effects discernible in the data.

(1) Variation in the size and condition of parental cysts. This depended upon the size of the sample from which a single cyst had to be chosen, either to initiate or maintain a line. As can be seen from Table 2.2 and 2.3, the percentages of cysts which failed to reproduce or reproduced poorly was greatest when the choice of parental cysts was restricted to one in five or less. This effect was more evident in the first inbred generation, i.e. when the parental cysts came from the field and so varied greatly in condition, than in the second inbred generation (Table 2.3), when the parental cysts were all of the same age and had developed on plants grown under glass. In either generation, when a cyst could be chosen from ten or more, the percentage of failures was reasonably constant at ten percent or less, and the range in numbers of new cysts produced was similar.

(2) Periodicity in the hatchability of eggs. The controversial subject of egg dormancy in H. rostochiensis was reviewed by Shepherd (1962), who established later (Shepherd and Cox, 1967) that the eggs definitely begin to enter a state of diapause as the cysts ripen. She found that diapause was less complete and of shorter duration when cysts were removed from the field and stored dry. Under these conditions, the period of minimum hatch in vitro lasted for about two months, namely the third or fourth months of storage.

TABLE 2.2.

Percentages of single-cyst lines yielding numbers of new cysts within certain limits, related to the number of cysts in the batches from which the founder cysts were selected. Data for first inbred generation of cysts.

No. of cysts in a batch collected at a site in the field.	No. of batches.	Yields of cysts in single-cyst culture. (cysts of S1 generation).									
		0	1-5	6-10	11-20	21-30	31-40	41-50	51-100	101-200	201->
1-5	236	41	23	5	5	5	3	5	10	2	-
6-10	65	17	25	11	17	3	8	5	10	6	-
11-20	74	7	22	9	23	11	7	8	11	3	-
21-30	48	10	21	10	13	10	17	-	19	-	-
31-40	51	10	31	10	18	8	4	-	20	-	-
41-50	34	8	21	8	28	13	3	3	13	5	-
51-100	95	9	16	18	9	8	9	7	19	3	-
101-200	62	5	13	10	10	6	11	6	27	10	2
201->	13	8	8	8	16	-	31	8	8	16	-

TABLE 2.3.

Percentages of single-cyst lines yielding numbers of new cysts within certain limits, related to the number of cysts in the batches from which the founder cysts were selected. Data for second inbred generation of cysts.

No. of cysts in a batch regenerated in the S1 generation	No. of batches.	Yields of cysts in single-cyst culture. (cysts of S2 generation).									
		0	1-5	6-10	11-20	21-30	31-40	41-50	51-100	101-200	201->
1-5	159	15	33	8	7	8	4	8	17	2	
6-10	57	4	30	12	19	4	9	2	12	2	
11-20	73	4	22	8	22	12	7	10	10	5	
21-30	49	8	20	12	13	12	16	-	16	-	
31-40	51	10	29	10	18	6	6	-	22	-	
41-50	39	5	21	8	28	13	8	-	8	10	
51-100	89	8	15	18	10	9	13	8	19	-	
101-200	63	2	16	6	11	10	13	3	29	10	
201->	22	5	5	5	9	9	18	5	18	27	

Data relating to the production of the S2 generation of cysts from the eggs in a single S1 cyst per plant are presented in Table 2.4. The S1 cysts were obtained from two crops of potatoes which were grown under glass and dried off in June 1965 and April 1966. This difference in the date of collecting the parent cysts, together with the staggered dates of planting the following six crops, which supported the S2 generation, meant that the S1 cysts had been stored dry for periods ranging from 3 to 11 months before they were used as inoculum.

After dry storage for 9 to 11 months, S1 cysts produced a second generation of cysts at the cream or lemon stage after 7 to 9 weeks. Since this was not much longer than the minimum time of about six weeks required for a larva to reach this stage of development (Franklin 1951), the eggs in these cysts were not in ~~a~~ diapause; they must have begun to hatch on receipt of hatching stimulus from the first roots produced.

S1 cysts which had been stored dry for 3 and 4 months required 10 to 16 weeks to produce S2 cysts at the cream or lemon stage. Since this storage period coincided exactly with the period over which Shepherd and Cox (1967) obtained minimum hatch, it must be concluded that the S1 cysts used to infect the fourth and fifth crops were in diapause at the date of planting. The eggs probably lay dormant for up to 9 weeks before they began to hatch, which agrees with the duration of the period of minimum hatch as observed by Shepherd and Cox.

It follows that the eggs in the S1 cysts used to infect the

first, second and third crops had passed through diapause. These crops yielded 66 - 80% more cysts than the fourth and fifth crops. The poor yield of cysts in the sixth crop was possibly due more to poor growth of the host plants in mid-winter than to diapause, because the parent S1 cysts had been stored for nine months before they were used as inoculum.

It can be seen from Table 2.4 that the percentage of single-cyst lines which reproduced, to the extent of producing at least one new cyst, did not vary appreciably throughout the year. This can be attributed to the fact that the growing period of the various crops was not standardised, but depended upon the time required for cysts to appear at the cream or lemon stage. The difference in generation time was accepted as such, and was not allowed to interrupt the work of producing and testing single-cyst lines throughout the year. This was completed before the results of Shepherd and Cox were published (1967); only then, in retrospect, did it become obvious that the difference in generation time was almost certainly due to diapause.

Hatching in any cyst continues over a long period and is frequently not completed in a season (Ellenby 1956). Roots are invaded as they grow, and so the cysts on any plant or in any batch always vary in age to some extent. This could be associated with variation, at a given time, in stage and subsequent duration of diapause between cysts of the same batch.

In this way, diapause could be held responsible for much of the extreme variation in the numbers of cysts produced in single-

TABLE 2.4

Data relating to the production of the S2 generation of cysts from the eggs in a single S1 cyst per plant

Crop	I	II	III	IV	V	VI
No. of plants	1428	1440	1457	1472	1664	1496
Date planted	14th March 1966	12th April 1966	19th May 1966	30th June 1966	4th July 1966	20th Dec. 1966
Date harvested	2nd May 1966	6th June 1966	17th July 1966	5th Sep. 1966	29th Oct. 1966	21st Feb. 1967
No. of pot contents investigated by flotation	576	648	600	672	234	528
Date of collection of S1 cysts	June 1965	June 1965	June 1965	April 1966	April 1966	April 1966
Age of S1 cysts at date of planting	9 months	10 months	11 months	3 months	4 months	9 months
Percentage of S1 cysts reproducing *	89·0	95·5	85·4	89·1	84·0	78·5
Time taken for S2 generation cysts to mature; in weeks.	7	9	8	10	16	9
Mean S2 cysts produced per plant	27·27	45·43	29·97	9·20	9·15	8·09

(Contd. P.45)

* Refers to pot contents investigated by flotation.

TABLE 2.4 (Contd.)

	I	II	III	IV	V	VI
Field populations involved	Burnside Barebanes Spittal	Spittal Archerfield 14 Archerfield 15	Archerfield 15 Ferrygate Kettle	Pitlethie Blackhall	Blackhall Woodbank Mt. Hallow A " " B " " D " " E " " F	Burnside Barebanes Spittal Archerfield 14 Archerfield 15 Ferrygate Kettle Pitlethie Blackhall Woodbank Mt. Hallow A " " B " " D " " E " " F

cyst cultures, as recorded in Table 2.1, and as reported by Gemmell (1940); Ellenby (1943) and Fenwick (1943).

(3) Possible genetic variation. It was envisaged that some inbred lines might prove to be more prolific than others, especially if H. rostochiensis is subject to inbreeding depression, as found by Howard (1966). Howard's findings tend to suggest that H. rostochiensis has some deleterious, recessive genes, such as might be reduced in frequency, as a result of inbreeding, whenever a colony is founded by a single cyst. It will be shown in the following section that one recessive gene, deleterious to some extent, is probably maintained by hetrozygous advantage in some populations.

In the first and second inbred generations, respectively, 9·7% and 5·4% of the parental cysts gave rise to more than 100 new cysts. The distribution of these high yielding lines in the two generations is emphasised by shading in Maps 1b to 15b. No particular significance need be attached to their distribution at present because it may reflect a lack of diapause rather than genetic variation. Probably inbreeding would have to be continued for several generations more, taking care to use cysts out of diapause, before any such genetic variation could be established.

It is possible that diapause itself is under genetic control and subject to different selection pressure under different conditions. In early potato growing fields such as Archerfield 15 (Map 5b), where high yielding lines were most frequent, there would be little possibility of a second generation arising and

possibly no need for diapause; hatching is unlikely to occur in cysts which are still only partially mature when a crop is lifted. It is assumed that one advantage of diapause is that it may prevent wastage due to larvae hatching late in the season, when the host crop would be senescent or dead before they could develop to maturity.

SECTION III

THE DISTRIBUTION OF PATHOTYPES WITHIN FIELDS

THE DISTRIBUTION OF PATHOTYPES WITHIN FIELDS.

Introduction

It is essential to clarify what a pathotype is and to consider systems of denoting pathotypes.

Classification of pathotypes.

A pathetype of potato cyst nematode is a group of biotypes or individuals possessing a certain resistance-breaking property or specificity. The term specificity derives from the fact that the major resistance genes used to differentiate pathotypes confer pathotype-specific resistance. As far as is known, pathotype-specific resistance inhibits female development, virtually suppressing cyst formation in some cases, but does not prevent root invasion or the development of males. This has been established in the case of resistance to H. rostochiensis in subsp. andigena (Jones, 1954). Other examples of resistance acting primarily against female development are known, e.g. resistance to Meloidogyne incognita in Lycopersicon peruvianum (Peacock, 1959) and Heterodera avenae in Hordeum vulgare, (Cotton, 1967).

In H. rostochiensis as far as is known, this pattern of restricted development of females and less restricted development of males has not yet been demonstrated in resistant potatoes bred from S. multidissectum, S. sanctae-rosae or S. spegazzinii, in which it is apparently taken for granted. It is possible that resistance has the effect of altering the sex ration in favour of males, since the sex ratio in potato cyst nematode can vary within

wide limits according to conditions (Ellenby, 1957); it may even cause sex-reversal (Turdgill, 1967). Males probably require less nutrition than the females, judging from the differences in mass between a female full of eggs and a male.

These aspects of resistance are the subject of considerable research beyond the scope of this thesis, which is concerned solely with the measurement of resistance in terms of cyst production, and the classification, distribution, and genetics of pathotypes as differentiated by means of potatoes incorporating pathotype-specific resistance. Obviously a system of denoting pathotypes is required, preferably a system capable of general acceptance.

Various nomenclatures have been proposed (Howard, 1959b; Dunnett, 1960a; Huijsman, 1962). Dunnett suggested using the numerical system which has been adapted internationally (Black, et al., 1953) for denoting strains of Phytophthora infestans, the fungus causing late blight of potatoes. This system caters for any number of resistance genes, singly and in all combinations. For instance, using four resistance genes, Black et al. (1953) produced the sixteen possible genotypes, taking the genes one at a time, two at a time and so on, disregarding different dosages of the same gene, and identified the 16 corresponding races of blight. This system is now considered unsuitable for H. rostochiensis because it is clear that certain types of specificity of resistance-breaking cannot be combined effectively in the same biotype (Dunnett and Bedi, Appendix 2). In other words, specificity in the late blight fungus is apparently always controlled by

independently acting genes, but not in the potato cyst nematode, in which one type of specificity may be dominant over another. Therefore a system of using single code letters to denote pathotypes is preferred. This simple system shelves all considerations of genetic recombination of specificity genes. As applied to P. infestans, in the example given above, 16 code letters would be required, instead of combinations of four numerals, presumably representing four specificity genes.

Table 3.1 gives the code letters denoting specificity according to a circular issued as a result of a meeting between British, Dutch and German potato breeders at Gross Lüsewitz, East Germany, in 1967, and the code letters which it is proposed to use in Great Britain as a result of verbal agreement reached at an "Open" Conference sponsored by the National Agriculture Advisory Service in London, 1967. Obviously, very little adjustment is required to bring the two systems into line, but this is a matter for further negotiation between breeders and not to be discussed here. For the purpose of this thesis, the N.A.A.S. system is used. The numerical system is given simply for comparative purposes.

TABLE 3.1.

Designation of pathotypes.

Pathotype		System		
		Gross-Lüsewitz	N.A.A.S (British)	Numerical system
Breaks no resistance		A	0	0
Breaks resistance	ex. S. multidissectum.	-	A	2
" "	ex. subsp. andigena	B	B	1
" "	ex. S. kurtzianum	C	-	-
" "	ex. S. vernei	D	-	-
" "	ex (S. multidissectum) (X) (subsp. andigena)	E	E	(1,2)*

* No longer used: equivalent to A, not E, (see Appendix 2).

Materials

Crops of the required resistant varieties and Craigs Defiance were grown in plots at the Scottish Plant Breeding Station and were maintained from year to year in a reasonably virus-free state by the removal of infected plants during the growing season. Each year part of the crop was put into cold storage to ensure a supply of tubers for planting in summer and autumn, so that tests of resistance could be set up throughout the year.

Varieties of a potato possessing resistance ex. S. kurtzianum and S. vernei, referred to in Table 3.1 were not included. S. kurtzianum does not figure at present in breeding in Great Britain, and the material was not available in quantity; S. vernei is used

only as a source of possible nonspecific or general resistance in Britain.

Two species of potato not included in Table 3.1., namely S. sanctae-rosae and S. spegazzinii, are used as sources of pathotype-specific resistance in Britain. At the start of this investigation, S. sanctae-rosae was bracketed with S. multidissectum because both species were known to have a major gene conferring resistance to pathotype B, but not pathotype A (Dunnett, 1961, 1964; Jones and Pawleska, 1963). S. spegazzinii was bracketed with subsp. andigena, because both species were known to have a major gene conferring resistance to pathotype A but not pathotype B (Dunnett, 1960a; Ross, 1962). This bracketing can be seen in Table 3.2. which lists the origins of resistance in the seven classes of potato which were actually tested against the S2 generation of the single-cyst lines representing the fifteen intensively sampled fields.

Table 3.2.

Origins of resistance and interaction with pathotype

Operative resistance gene.	Origin	Collection number	Interaction with pathotype O	A	B	E
-	Solanum tuberosum subsp. tuberosum		+	+	+	+
H1	S. " " andigena)	C.P.C.1673	-	-	+	+
Fa	S. spegazzinii)	E.B.S. *	-	-	+	+
H2	S. multidissectum)	P.H. 1366	-	+	-	+
H2	S. sanctae-rosae)	P.H. 328	-	+	-	+
H1H2	subsp. andigena X S. multidissectum)		-	-	-	+
H1H2	subsp. andigena X S. sanctae-rosae)		-	-	-	+

- = Resistant
+ = Susceptible

* Received from H.Ross, Max-Planck Institute, Cologne.

In this context, "S2 generation" refers to the progenies of eggs enclosed in S1 cysts, and "single-cyst line" means the family of S1 cysts produced on a plant of Craigs Defiance by the progeny of a single cyst from the field.

One plant of each of the seven classes of potato listed in Table 3.2 was tested against each line, which had therefore to comprise at least seven S1 sister cysts at this stage. A total of approximately 900 lines which met this requirement was used in the investigation of the distribution of pathotypes.

Methods

It follows that a total of approximately 6,300 single-cyst cultures were set up in 1966, in seven parallel, "sister-cyst" series. It was impossible to recover cysts by flotation from all this material, because flotation is a time consuming technique. It was decided to carry out a preliminary inspection of root-balls, and to extract cysts only from pots planted with Craigs Defiance or when the highest degree of accuracy was desirable.

In order to test the efficacy of pot-ball scoring, i.e. counting cysts in situ on the roots, the number of cysts seen on the roots of a trial batch of material was compared with the number extracted by flotation (Table 3.3). The correlation was reasonably good when the plants had more than 5 cysts visible on the root mat, as was to be expected, because the pots were so small that a large proportion of the rootsystem was visible. At this level the

correlation was probably better than that observed by Jones and Pawleska (1963), using larger pots. It was clear, however, that many plants showing no cysts on the root-mats were not in fact cyst-free. In the susceptible range (Tables 3.3 A and B) about 72% of the plants showing no cysts on the roots yielded cysts by flotation, as many as over 50 cysts in a few cases. In the resistant range (Table 3.3 C), 63% of the plants showing no cysts on the roots yielded one or more cysts, usually one new cyst only, but this was highly significant since it was tantamount to maintenance of the initial population for one generation, the inoculum for each plant having been provided by only one cyst. Therefore, because the variation in cyst production over the susceptible range was so great in any case (Table 3.3 A) it was not important to assess total cyst production very accurately at this level, and flotation was used mainly in cases when visible cyst production was low, or not apparent from inspection of the roots.

Inspection of the roots of any batch of material was deferred until cysts were visible on the roots of plants of Craigs Defiance planted and infested under the same conditions.

TABLE 3.3.

Correlation between numbers of cysts counted on the external root-mat and total number of new cysts formed in 2-inch pots

TABLE 3.3 A Host - Craigs Defiance

Cysts counted on root-mat	Cysts recovered by flotation: 0	1-5	6-10	11-15	16-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100	100 >
0	33	77	15	11	5	8	4	2	2	2	2	1	-	-
1-5	-	7	4	9	6	3	4	1	1	1	1	-	1	-
6-10	-	5	2	5	3	8	5	8	2	-	-	-	1	1
11-15	-	3	2	1	1	5	10	2	3	-	1	3	1	2
16-20	-	-	2	-	3	3	4	8	3	3	2	1	-	4
21-30	-	-	-	2	3	5	5	8	7	4	6	1	3	3
31-40	-	-	-	-	2	3	9	3	4	6	6	2	3	4
41-50	-	-	-	-	1	3	3	-	3	5	3	4	3	3
51-60	-	-	-	-	-	1	-	-	1	3	-	2	2	7
61-70	-	-	-	-	-	-	-	-	-	2	-	-	1	1
71-80	-	-	-	-	-	-	-	-	-	-	-	1	1	1
81-90	-	-	-	-	-	-	1	-	-	-	-	1	-	-
91-100	-	-	-	-	-	-	-	-	-	-	-	-	-	-

number of plants

TABLE 3.3 B Host X *S. multidissectum* and X *S. sanctae-rosae*.

Cysts counted on root-mat	Cysts recovered by flotation: 0	1-5	6-10	11-15	16-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100	100 >
0	28	20	12	7	6	7	6	2	2	2	-	-	-	-
1-5	-	10	6	6	9	4	4	3	1	2	1	-	1	-
6-10	-	6	6	5	4	10	5	5	3	2	1	-	-	1
11-15	-	2	8	1	4	5	4	2	5	1	3	-	1	1
16-20	-	3	3	2	9	5	4	9	1	2	1	3	1	-
21-30	-	-	3	6	6	19	10	6	10	9	6	2	3	3
31-40	-	-	4	1	2	9	13	8	7	5	3	4	-	2
41-50	-	-	-	1	4	5	6	7	1	9	1	2	-	1
51-60	-	-	-	-	-	-	1	3	6	2	2	2	1	5
61-70	-	-	-	-	-	-	1	-	-	3	-	3	1	2
71-80	-	-	-	-	-	-	1	-	-	-	-	-	2	1
81-90	-	-	-	-	-	-	-	-	-	1	-	-	-	2
91-100	-	-	-	-	-	-	-	-	-	-	-	-	-	-

number of plants

TABLE 3.3 (Contd.)

TABLE 3.3 C Host X subsp. andigena and X S. spegazzinii.

Cysts counted on root-mat	Cysts recovered by flotation										
	0	1	2	3	4	5	10	20	30	40	50
0	128	120	50	16	15	6	7	5	-	1	-
1	1	2	4	4	2	1	3	-	-	-	-
2	-	4	2	1	-	-	2	-	-	-	-
3	-	-	-	1	-	-	1	-	-	-	-
4	-	-	-	-	1	-	-	1	-	-	-
5	-	-	-	-	-	-	-	-	-	-	-
6-10	-	-	-	-	-	-	-	-	-	-	-
11-20	-	-	-	-	-	-	-	-	-	-	-
21-30	-	-	-	-	-	-	-	-	-	-	-
31-40	-	-	-	-	-	-	-	-	-	-	-
41-50	-	-	-	-	-	-	-	-	-	-	-
	number of plants										

Results.

Pathotype maps: These are interleaved with the maps of population density at the end of the section (Map Index, page 85), so that distribution of a particular pathotype can be seen in relation to variation in overall population density. The pathotype maps were constructed by using lines of different slopes and spacing to represent reproduction on the six classes of resistant potato (Table 3.2) and Craigs Defiance.

Pathotype E: The two complete series of single-cyst cultures on H1H2 plants stemming from adg[1] X mlt[2] and adg X sct[3] produced no new cysts in a position to be seen on the root-mats. Absence of

1. adg = subsp. andigena)
2. mlt = S. multidissectum) Abbreviations proposed by Simmonds (1963 b).
3. sct = S. sanctae-rosae)

cysts was confirmed by flotation of pot contents in the case of all H1H2 plants tested against lines from Archerfield 14, a total of 64 plants, divided equally between the series adg X mlt and adg X sct.

Many lines had sister cysts which reproduced in plants incorporating the H1 and H2 resistance genes separately but not when the genes were combined in H1H2. Absence of cysts in such cases was particularly significant and was always confirmed by flotation.

It was concluded that pathotype E, by definition the only pathotype capable of encysting in H1H2 plants, was not represented in the populations being investigated.

Pathotype A: H2 plants ex mlt and sct were bracketed together in Table 3.2 as having indistinguishable resistance which operated against pathotype B but not pathotype A. Before proceeding further it was necessary to consider the possibility of subdividing pathotype A, which was essentially a question of distinguishing between resistance ex mlt and ex sct.

Table 3.4 compares cyst production in the three parallel series of single-cyst cultures on Craigs Defiance, H2 plants ex mlt and H2 plants ex sct.

The data for Craigs Defiance are those already presented in Table2.1of Section 11, in which possible causes of the extreme variation in the reproduction of lines from the same field were discussed. This variation was not attributed to genetic causes, except possibly genetically controlled diapause, because Craigs Defiance or any other variety of subsp. tuberosum is accepted as a universal host for all European populations of the potato cyst nematode.

Cyst reproduction in the two series of H2 plants ex mlt and ex sct varied to the same extent as in Craigs Defiance, although additional variation due to genetic causes might have been expected because the capacity to break resistance is a genetic character, in this instance typical of pathotype A. The frequency of this pathotype, as calculated according to Jones' method averaged 64% for mlt and 71% for sct over all the lines. Possibly the yield of cysts in the H2 series ex mlt and ex sct was affected considerably less by variation in the frequency of pathotype A than by diapause.

There was a positive correlation between the field means for the numbers of cysts produced in the two H2 series, ex mlt and ex sct ($r = 0{\cdot}849$, significant at ·01% level). Furthermore, when the percentage of lines producing one or more cysts was considered, (Table 3.5) a positive correlation was again statistically significant ($r = 0{\cdot}849$, significant at 0·01% level).

This indicates that the variation in the numbers of cysts produced and also in the percentage of cysts reproducing, tended to be consistent from mlt series to sct series, suggesting,

(a) Some factor or some complex of factors was responsible for a real difference between the lines from different fields.

(b) The resistance in H2 plants ex mlt and H2 plants ex sct was indistinguishable with respect to these lines.

There was therefore no question of subdividing pathotype A.

In the pathotype maps, no distinct patterns are to be seen in the distribution of pathotype A. The areas where a single-cyst line

TABLE 3.4.

Cyst production in the series of single-cyst cultures on H2 plants ex S. multidissectum and ex S. sanctae-rosae and on Craigs Defiance

Field Population	1	2	3	4	5	6	7
Burnside	mlt.	40	13·85	16·5	108·0	53·0	
	sct.	35	24·94	18·5	72·0		95·4
	C.D.	38	26·13	26·6	101·9		
Barebanes	mlt.	36	21·96	21·3	78·2	97·2	
	sct.	31	28·29	24·4	77·1		125·1
	C.D.	33	22·60	23·7	10·7		
Spittal	mlt.	90	23·96	23·0	91·6	74·6	
	sct.	80	32·61	24·0	82·9		101·5
	C.D.	93	32·12	25·3	78·7		
Archerfield 14	mlt.	34	51·53	33·0	66·4	110·8	
	sct.	32	44·15	22·8	51·3		94·9
	C.D.	35	46·51	30·1	63·8		
Archerfield 15	mlt.	64	51·14	36·7	59·9	68·3	
	sct.	62	66·17	30·7	51·1		88·3
	C.D.	68	74·90	41·9	55·9		
Ferrygate	mlt.	63	18·95	18·4	99·4	67·8	
	sct.	38	26·19	22·6	94·5		93·5
	C.D.	68	28·00	36·8	130·0		
Kettle	mlt.	40	16·34	16·1	93·0	44·5	
	sct.	33	25·48	19·4	91·3		69·4
	C.D.	31	36·70	24·3	66·2		
Pitlethie	mlt.	92	6·95	9·0	111·0	67·4	
	sct.	88	7·84	8·3	102·5		76·0
	C.D.	89	10·31	14·4	139·8		
Woodbank	mlt.	46	3·88	5·6	145·6	37·8	
	sct.	45	4·75	4·4	92·6		46·2
	C.D.	42	10·26	9·2	89·2		
Blackhall	mlt.	112	6·25	7·5	107·5	82·2	
	sct.	102	5·85	6·3	106·0		76·9
	C.D.	102	7·60	9·4	102·5		

[Contd. on P.60....

Key to columns: 1. Host material, mlt = Clones incorporating H2 resistance ex S. multidissectum.

sct = Clones incorporating H2 resistance ex S. sanctae-rosae.

C.D. = Universal susceptible host, Craigs Defiance.

2. Number of single-cyst cultures.
3. Mean cyst production.
4. Standard deviation.
5. Coefficient of variation.
6. Cyst reproduction on mlt relative to Craigs Defiance = 100
7. Cyst reproduction on sct relative to Craigs Defiance = 100

TABLE 3.4 (Contd.)

Field Population	1	2	3	4	5	6	7
Mount Hallow A	mlt.	38	2·74	3·9	144·4	22·6	
	sct.	38	2·30	6·8	200·0		19·0
	C.D.	33	12·10	14·7	121·0		
Mount Hallow B	mlt.	16	1·10	3·4	64·1	18·3	
	sct.	16	2·45	4·6	73·0		40·8
	C.D.	12	6·00	8·9	148·0		
Mount Hallow D	mlt.	34	5·32	6·1	98·3	59·9	
	sct.	34	5·94	7·5	108·9		66·8
	C.D.	28	8·88	8·5	95·5		
Mount Hallow E	mlt.	26	7·23	9·3	113·9	55·2	
	sct.	25	5·52	6·3	91·7		42·1
	C.D.	23	13·10	16·6	126·7		
Mount Hallow F	mlt.	29	8·17	9·2	100·6	109·2	
	sct.	33	4·48	4·5	78·9		59·8
	C.D.	27	7·48	9·4	125·0		
Means	mlt.		15·95	14·60	98·76	64·6	71·3
	sct.		19·10	14·07	91·58		
	C.D.		22·84	18·18	96·99		

Key to columns:

1. Host material, mlt. = Clones incorporating H2 resistance ex S. multidissectum.
   sct. = Clones incorporating H2 resistance ex S. sanctae-rosae
   C.D. = Universal susceptible host, Craigs Defiance.
2. Number of single-cyst cultures.
3. Mean cyst production.
4. Standard deviation.
5. Coefficient of variation.
6. Cyst reproduction on mlt relative to Craigs Defiance = 100
7. Cyst reproduction on sct relative to Craigs Defiance = 100

TABLE 3.5

Frequency (percent) of single-cyst lines reproducing on S. multidissectum, S. sanctae-rosae and Craigs Defiance.

Field Population.	Craigs Defiance		S. multidissectum		S. sanctae-rosae	
	No. of lines inoculated	% reproducing	No. of lines inoculated	% reproducing	No. of lines inoculated	% reproducing
Burnside	38	97·36	40	90	35	93·6
Barebanes	35	94·5	37	96·7	31	97·0
Spittal	97	96·9	99	86·7	83	86·3
Archerfield 14	35	100·0	36	96·1	33	98·6
Archerfield 15	68	100·0	69	98·0	62	100·0
Ferrygate	75	90·6	63	84·1	38	91·0
Kettle	37	94·5	40	82·5	33	85·0
Pitlethie	95	93·6	94	87·2	88	93·6
Woodbank	49	87·7	46	73·9	45	88·5
Blackhall	120	84·1	110	83·5	102	87·0
Mount Hallow A	42	80·4	43	74·4	43	78·6
" " B	18	66·6	20	75·0	18	77·7
" " D	36	77·7	38	79·0	36	80·7
" " E	26	88·7	33	72·7	27	74·4
" " F	35	78·7	27	81·5	35	74·2

reproduced on H2 plants ex mlt but not on H2 plants ex sct, or vice versa, are scattered at random and probably represent reproductive failure for various reasons almost certainly not genetic, as has already been established.

Pathotype 0: Since pathotype 0 does not encyst, by definition, in H2 plants or H1 plants, any evidence for its existence depended on the difference between the percentages of lines reproducing in Craigs Defiance and in either H1 or H2 plants. From field to field, the percentage of lines reproducing on Craigs Defiance was often greater than in H2 plants ex mlt or ex sct (Table 3.6), but generally the difference was negligible, only 3·4% greater than in H2 plants ex mlt and 0·2% greater in H2 plants ex sct.

This suggested that pathotype 0 was absent or negligible in frequency. Nevertheless, if even one line could be shown to behave consistently as pathotype 0, this would be sufficient to establish the existence of pathotype 0.

Additional cysts were available which belonged to 144 S1 families of sister cysts which had reproduced on Craigs Defiance only in the series of single-cyst cultures carried out in 1966 on the seven categories of potato material listed in Table 3.2. In December of the same year, three cysts from each family were used to set up a single-cyst culture on Craigs Defiance, an H1 plant ex adg, and an H2 plant ex mlt.

TABLE 3.6.

The difference in cyst production (percent) between Craigs Defiance and H2 resistance plants ex S. multidissectum and S. sanctae-rosae

Field Population	Single cyst lines (percent) reproducing on Craigs Defiance	The difference in cyst production (percent) on, S. multidissectum	S. sanctae-rosae
Burnside	97·4	-7·4	-3·8
Barehanes	94·5	+2·0	+3·0
Spittal	96·9	-10·2	-10·6
Archerfield 14	100·0	-4·0	-1·4
Archerfield 15	100·0	-2·0	0·0
Ferrygate	90·7	-6·4	+0·3
Kettle	94·6	-12·2	-9·5
Pitlethie	93·7	-6·7	-0·1
Woodbank	87·8	-13·7	+0·7
Blackhall	84·1	-1·0	+2·9
Mount Hallow A	80·5	-6·1	-1·9
" " B	66·7	+8·4	+11·0
" " D	77·8	+1·2	+2·9
" " E	88·9	-16·1	-14·7
" " F	78·8	+2·7	-4·6
Arithmetical means	87·4	-3·4	-0·2

After a lapse of nine weeks, one or more apparently new cysts were recovered by flotation from 127 plants of Craigs Defiance, 130 H2 plants ex mlt, and 7 H1 plants ex adg (Table 3.7). Since failure to reproduce on Craigs Defiance could not be attributed to resistance in the host, the same could be said of failure to reproduce in H2 plants ex mlt in this instance, because the percentages of S1 cysts failing to reproduce was

practically the same in these two series. Therefore it was almost certain that none of the S1 cysts placed in contact with the H2 plants had contained a progeny consisting entirely of pathotype O. Since these cysts came from the only single-cyst, inbred lines which could reasonably be suspected of including pathotype O,it could be inferred that cysts containing progenies consisting entirely of pathotype O did not occur in any other lines from any of the fields investigated.

As can also be seen from Table 3.7, the mean cyst production on H2 plants ex mlt was greater than on Craigs Defiance, thus excluding the possibility that pathotype O was even segregating to any appreciable extent within the progenies of individual cysts.

There was no need to consider pathotype B in arriving at these conclusions, although pathotype B encysts in potatoes such as Craigs Defiance and in H1 plants ex adg but not in H2 plants ex mlt. The seven H1 plants on which new cysts were recovered never supported more than two new cysts per plant. This lends support to the submission that it was not necessary to consider pathotype B; it was evidently too infrequent to be a significant cause of failure to reproduce in any of the H2 plants ex mlt.

TABLE 3.7

Results of the re-test of single-cyst lines, suspected of behaving like pathotype 0

Field Population and number[1]		Number of cysts reproduced on Craigs[2] Defiance	Number of cysts reproduced on sp. *andigena*.[3]	Number of cysts reproduced on *S. multidissectum*.[4]
Burnside	6	7	0	9
	12	0	0	0
	36	2	0	20
	48	1	0	2
	49	2	0	0
	65	10	0	3
	78	20	0	8
	79	2	0	14
	84	1	0	5
	90	16	0	0
	95	0	0	10
	99	0	1	2
	102	0	0	7
Barebanes	11	8	0	2
	13	25	0	115
	14	14	0	11
	33	12	0	21
	39	2	0	12
Spittal	24	0	0	0
	41	15	0	13
	45	12	0	5
	49	12	0	19
	52	16	0	0
	117	1	0	2
	122	12	0	5
	124	3	0	14
	127	1	0	0
	130	2	0	1
	131	2	0	43
	151	2	0	5
Archer-field 14	51	22	0	67
" 15	54	3	0	1
	9	8	0	5
	24	0	0	12
	55	40	0	38
	62	6	0	13
	63	5	0	27
	66	25	0	28

TABLE 3.7 (Contd.)

	1	2	3	4
Ferrygate	1	1	0	25
	2	2	0	17
	8	21	0	28
	14	10	0	52
	24	16	0	10
	26	15	0	3
	33	10	0	25
	36	23	0	2
	63	15	0	20
	65	5	0	10
	67	0	0	15
	72	1	0	12
	73	31	0	6
	77	53	0	32
	79	5	0	0
	81	26	0	40
	85	14	0	25
	90	3	0	7
	91	4	0	7
	94	20	0	20
	96	35	0	19
	117	7	0	9
Kettle	1	11	0	8
	3	8	0	27
	16	33	0	18
	17	15	0	63
	20	3	0	20
	42	10	0	35
	44	16	0	38
	45	10	0	32
Pitlethie	1	4	0	12
	2	0	0	3
	3	0	0	0
	9	22	0	10
	11	0	0	0
	13	0	0	3
	14	22	0	25
	15	1	0	3
	16	1	0	19
	18	2	0	7
	22	7	0	11
	27	6	0	35
	28	4	0	5
	30	1	0	7
	31	1	0	4
	34	2	0	6
	35	5	0	21

TABLE 3.7 (Contd.)

1	2	3	4
40	0	0	17
49	10	0	11
50	6	0	22
51	8	0	9
53	30	0	53
57	28	0	17
59	0	0	0
62	15	0	29
68	0	0	8
69	1	0	3
73	3	0	6
79	6	0	0
84	0	0	3
86	20	0	43
87	6	0	19
Blackhall 4	9	0	11
5	0	0	3
6	3	0	2
7	27	1	10
63	3	0	0
87	0	0	9
88	9	0	9
89	10	0	36
101	2	0	13
117	6	0	36
120	0	0	2
126	12	0	25
129	44	0	36
Woodbank 3	26	0	6
7	21	0	28
10	1	0	15
17	8	0	1
32	9	2	4
38	1	0	8
48	16	2	7
54	10	0	0
58	14	0	3
65	19	0	20
Mount 8	15	0	14
Hallow A 16	13	0	19
24	1	0	1
29	37	1	24
37	2	0	10

TABLE 3.7. (Contd.)

	1	2	3	4
Mount Hallow B	6	3	0	7
" D	11	25	1	1
	3	27	0	17
	10	6	0	0
	16	16	0	28
	33	6	0	5
" E	2	11	0	5
	7	16	0	6
	11	1	1	1
	14	4	0	6
	16	2	0	9
	20	1	0	20
" F	7	49	0	45
	14	20	0	21
	27	37	0	19
Mean		10·47		14·90

Pathotype B: Pathotype B was present to some extent in the fields which were investigated, judging from the production of cysts on H1 plants ex adg and on Fa plants ex spg[1] (Table 3.8) which were bracketed together as having indistinguishable resistance (Table 3.2) at the beginning of this section in the thesis.

The percentage of lines reproducing on H1 plants was fairly low and never exceeded 70% for any one field (Table 3.8). In addition, the average number of cysts produced by single-cyst progenies on H1 plants ex adg and on Fa plants ex spg was very low (Table 3.9). In fact, 59·24% of lines which reproduced on

1. spg = S. spegazzinii. Abbreviation proposed by Simmonds (1963b).

Hl plants ex adg and Fa plants ex spg. produced only one new cyst. Even this, in single-cyst cultures, was more or less equivalent to population maintenance over one generation.

Turning to the pathotype Maps 1c to 15c (Map Index page 85) it is clear that the founder cysts of the single-cyst lines that produced one or more cysts on Hl plants ex adg or Fa plants ex spg, were certainly not distributed entirely at random within fields, but tended to come from adjacent sampling points, with the result that the maps show small to fairly large islands or patches of pathotype B within each infestation.

The maps also show that the lines which reproduced on Hl plants ex adg and the lines which reproduced on Fa plants ex spg, originated in islands which coincided to a large extent, which suggested:

(a) The resistance ex adg and ex spg had still to be treated as indistinguishable.

(b) The single-cysts or small numbers of cysts which developed on Hl plants ex adg and ex spg usually represented pathotype B and were not exceptional cysts of pathotype A.

The limited cyst production on Hl plants suggests that the single-cyst progenies were not fixed for specificity B but were probably segregating, either as a result of matings involving heterozygous or multiple matings with males of pathotype A and B.

The patches of pathotype B occurred mainly in areas of low

population density, notably in Spittal, Archerfield 15 and Ferrygate (Maps 3c, 5c and 6c), as can be verified from the interleaved maps showing pathotype distribution and population density in each field.

TABLE 3.8.

Frequency (per cent) of single-cyst lines reproducing on H1 resistant plants ex subsp. *andigena* and *S. spegazzinii*.

Field Populations	subsp. *andigena*.	*S. spegazzinii*
Burnside	3·92	0·00
Barebanes	7·30	23·52
Spittal	14·26	16·00
Archerfield 14	22·22	71·37
Archerfield 15	23·52	66·55
Ferrygate	3·80	33·75
Kettle	5·00	23·52
Pitlethie	2·15	-
Woodbank	4·16	-
Blackhall	0·90	2·20
Mount Hallow A	17·50	9·60
" " B	20·90	11·10
" " D	16·19	8·40
" " E	14·30	0·00
" " F	19·40	5·60

From this point onwards it is accepted, on a basis of the pathotype mapping, that the cysts which arose on the test plants ex adg were females of pathotype B. The genetic constitution of their progenies is another question, and is considered in the discussion of this Section, because any female of pathotype B could have been fertilised by males of pathotype A; the resistance of adg does not preclude the development of males of pathotype A.

TABLE 3.9.

Mean cyst production in single-cyst cultures on H1 plants ex subsp. *andigena* and Fa plants ex *S. spegazzinii*.

Field Populations	1	2	3	4	5
Burnside	adg	51	0·22	1·33	-
	spg	39	-	-	-
Barebanes	adg	39	0·30	1·60	-
	spg	33	1·15	1·61	-
Spittal	adg	100	0·82	2·35	14·00
	spg	87	1·57	1·97	6·50
Archerfield 14	adg	35	0·68	1·80	12·00
	spg.	33	2·84	3·24	8·00
Archerfield 15	adg	69	0·48	1·41	-
	spg	64	2·41	2·76	8·00
Ferrygate	adg	52	0·24	1·33	-
	spg	38	4·26	6·16	11·00
Kettle	adg	40	0·29	1·09	-
	spg	34	2·00	2·93	12·00
Pitlethie	adg	93	0·73	-	-
	spg	87	-	-	-
Woodbank	adg	48	0·12	1·50	-
	spg	45	-	1·00	-
Blackhall	adg	111	0·06	1·16	-
	spg	104	-	-	-
Mount Hallow A	adg	38	1·32	4·45	18·50
	spg	37	0·35	3·25	9·00
Mount Hallow B	adg	18	0·38	1·16	-
	spg	17	0·11	1·00	-
Mount Hallow D	adg	34	0·29	1·00	-
	spg	34	0·08	1·00	-
Mount Hallow E	adg	26	0·26	1·00	-
	spg	26	-	-	-
Mount Hallow F	adg	37	0·35	1·00	-
	spg.	33	0·06	1·00	-

Key to columns:

1. Host material, adg = Clones incorporating H1 resistance ex subsp. *andigena*.
   spg = Clones incorporating Fa resistance ex *S. spegazzinii*.
2. Number of single-cyst cultures.
3. Mean cyst production.
4. Mean cyst production excluding lines which failed to reproduce.
5. Mean cyst production excluding lines failing to produce less than 5 new cysts.

However, it was only necessary to know that the females were of pathotype B in order to proceed with the calculation of the mean frequency of pathotype B in the F2 generations of the lines from each field. For each field, the sum total of F2 cysts produced on Craigs Defiance was a measure of the size of the F2 population irrespective of pathotype, and the total of F2 cysts on the test plants ex adg was a corresponding measure of the size of the fraction which was pathotype B. The frequency of heterozygotes was calculated on a basis of the fact that specificity B is recessive to specificity A such that VaVa or Vavb gives specificity A, vbvb gives specificity B (Dunnett and Bedi, see Appendix 2). The results of calculations are presented in Table 3.10.

TABLE 3.10.

Calculation of the frequency of the recessive gene vb and heterozygotes (Vavb) from the frequency of vbvb biotypes (pathotype B) encysting on H1 plants ex adg.

Field Populations	No. of single cyst	Total cyst production on Craigs Defiance	Total cyst production on H1 plants ex.adg	Frequency of vbvb q^2	Frequency of heterozygotes $2q(1-q)$
Burnside	38	1003	7	1/143	1/6·5
Barebanes	33	1015	11	1/92	1/5·3
Spittal	93	3003	113	1/26	1/3·1
Archerfield 14	35	1866	40	1/46	1/3·9
Archerfield 15	68	5158	56	1/92	1/5·3
Ferrygate	68	2099	11	1/190	1/7·4
Kettle	31	1271	3	1/423	1/10·8
Pitlethie	89	980	5	1/196	1/7·5
Woodbank	42	431	7	1/61	1/4·4
Blackhall	102	940	5	1/188	1/6·9
Mount Hallow A	33	489	49	1/10	1/2·3
Mount Hallow B	12	107	7	1/15	1/2·5
Mount Hallow D	28	301	10	1/30	1/3·3
Mount Hallow E	23	304	7	1/43	1/3·8
Mount Hallow F	27	271	3	1/90	1/2·8
Means		1278·53	22·93	1/55·75 ± 29·1	1/4·3 ± 0·63

For all populations:-

$$q^2 = \frac{22{\cdot}93}{1278{\cdot}53} = \frac{1}{55{\cdot}75}$$

$$q = \frac{1}{7{\cdot}5}$$

$$2q(1-q) = \frac{2}{7{\cdot}5}\left(1 - \frac{1}{7{\cdot}5}\right) = \frac{1}{4{\cdot}3}$$

Discussion

The foregoing results have a bearing on certain questions which need to be discussed in a wider context.

(1) Are the indistinguishable resistance genes probably identical by descent? Extensive single-cyst testing failed to distinguish between the resistance conferred by the gene H1 ex adg (Toxopeus and Huijsman, 1953) and the gene Fa ex spg (Ross, 1962). It also failed to distinguish between the resistance conferred by the gene H2 ex mlt and the H2 gene ex sct (Dunnett, 1961, 1964). This vindicated the bracketing (Table 3.2) based on tests of resistance to multiple-cyst samples of the Boghall A population and the Duddingston B population (Dunnett, 1960a; Jones and Pawleska, 1963).

Jones and Pawleska (1963) agreed that the resistance ex spg (S. famatinae, Bitt. et Wittm.) "would probably be most useful against the same population as S. andigena", and did not differentiate between resistance ex mlt and ex sct. Most of their populations which encysted in material ex adg and ex spg. encysted also in material ex mlt and ex sct, and so, from the introduction to this section of the thesis, it can be deduced that many of them included pathotype E to some extent.

The single-cyst work clarified the relationship between resistance from the various sources, because it removed a valid objection to the bracketing in Table 3.2, namely that populations such as Boghall could comprise a mixture of two classes of biotypes,

one breaking resistance ex mlt and the other breaking resistance ex sct, from which it follows that material ex mlt and ex sct could be equally susceptible, but not uniformly susceptible, to the Boghall population as a whole.

It has been shown (Tables 3.4 and 3.5) that material ex mlt and ex sct was equally susceptible to a large number of pairs of single-cyst progenies, each pair of progenies having at least one common parent, and not many cysts which reproduced in material ex mlt did not have a sister cyst which reproduced in material ex sct (Tables 3.4 and 3.5). In general terms, therefore, it is reasonably certain that the two kinds of material were uniformly susceptible to pathotype A.

While it is probable that this general conclusion would be substantiated by a single-cyst analysis of any number of A populations some doubt about it would still remain, because if even a single line of potato cyst nematode were found to differentiate between resistance ex mlt and sct, this would be sufficient to establish that the dominant genes controlling the resistance of these species were different. There must come a point, however, when it is permissible to postulate that the resistance genes ex mlt and ex sct are identical by descent and it is suggested that this point has now been reached. Furthermore, if the rather difficult genetical study is undertaken, it is probable that these genes will be found to occur at the same locus.

By analogy with the foregoing discussion it is suggested

that the H1 gene ex adg and the Fa gene ex spg are also probably identical. There may be a very minor difference between these genes in that 'occasional' cysts of pathotype A appear more frequently on resistant material ex spg than on resistant material ex adg. If such a difference exists, it may be of the order of the somewhat doubtful difference between the H1 genes ex subsp. andigena clone C.P.C. 1685 and subsp. andigena clone C.P.C. 1673 (Huijsman, 1955, 1957; Cole and Howard, 1957).

It is not necessary to believe that the H1 gene arose de novo in adg, and is unique to adg, and that this gene is building up from its present low frequency in adg (Ellenby, 1952, 1954), in response to cultivation of the tetraploid species in South America and its resultant exposure to high populations of potato cyst nematode. The gene may have an older history, and may be identical with or closely related to the Fa gene ex spg, a diploid species of Series Tuberosa, the group which includes the progenitors of subsp. andigena (Simmonds, 1963a).

(2) Does pathotype 0 exist? No British population that could be classed as pathotype 0 has been reported in the literature although Jones and Parrott (1965) deduced that certain populations of mixed pathotypes probably included pathotype 0. Howard (1967) mentioned his difficulties in obtaining pathotype 0 and stated that there was no conclusive evidence for its existence.

The position in the Netherlands is confusing, since populations that multiply only on fully susceptible plants and not on differentially resistant plants bred from ktz,[1] vrn[2] and adg have been

1. ktz = S. kurtzianum Bitt et Wittm.) Simmonds (1963b)
2. vrn = S. vernei Bitt et Wittm.)

reported by Huijsman (1963) and Kort (1962), but these populations could only be classed as pathotype 0 if they failed to encyst also in differentially resistant material bred from mlt, sct and spg. This has not been ascertained, and so the following discussion is restricted to British populations. For reasons already given no distinction is made between adg and spg or between mlt and sct.

Jones and Parrott (1965) found that the sum of their estimated frequencies of biotypes breaking the separate or combined resistance of adg and mlt, came to less than 100%, leaving a residue which, if genetically distinct, could only be classified as pathotype 0. Their calculation of frequencies rested on the assumption that a given class of biotypes encysted as freely in differentially resistant material as in recessive potatoes such as Arran Banner. This is not necessarily the case, as Jones and Parrott themselves pointed out, because the H2 gene ex mlt has been shown to be associated with a variable level of general resistance to the potato cyst nematode. Any such general resistance in the H2 plants used by Jones and Parrott (1965) would have the effect of obviating any need to invoke pathotype A to account for the relatively greater cyst production which they observed on Arran Banner.

In theory, it is not possible to separate pathotype 0 from a mixture of pathotypes by mass selection, because pathotype 0 encysts, by definition, only in potatoes lacking all pathotype-specific resistance genes, as do all other pathotypes of the potato cyst nematode.

It should be possible, however, to isolate pathotype 0 from a mixture of pathotypes including it, by making use of the founder principle. Any field population including pathotype 0 might be expected to have zones within which the frequency of pathotype 0 was much higher than average for the whole population. It might also be expected that single cysts from such zones would occasionally found pure lines of pathotype 0. It has been shown (page 56) that 900 single cyst lines originating from as many sampling points in fifteen fields were tested and none was a pure line of pathotype 0. It is therefore extremely unlikely that pathotype 0 was even present in any of these lines, from any of the fields.

It is known (Appendix 2) that specificities A and B are controlled by allelomorphic genes, and this fact alone provides no genetical basis for the existence of pathotype 0. The hypothesis could be made to accommodate pathotype 0, if it could be shown to exist, by invoking epistatic dominance or a third allele at the specificity locus. However, on the grounds that the simplest hypothesis which accounts for all the known facts should be preferred, it is postulated that pathotype 0 does not exist, a conclusion now supported by genetic theory as well as the results of single-cyst investigations.

(3) <u>How is variability maintained in populations of potato cyst nematode</u>? Resistant varieties of potatoes bred from subsp. <u>andigena</u> had not been grown in any of the fields investigated; these

are not yet readily available to growers. None of the older varieties still grown in Britain has been found to be resistant to potato cyst nematode. Since the older European varieties of potato are supposed to be derived from common stock, a few clones of South American origin, (Simmonds, 1963a) it is improbable that any extinct European variety was resistant to potato cyst nematode.

Therefore in attempting to answer the question of how variability in potato cyst nematode is maintained, the effects of selection through resistant varieties can be disregarded during the 100 years or more (Jones, 1966) since the potato cyst nematode was introduced into Britain. In the fields which were investigated, the possibility of selection through S. nigrum, a weed possessing specific resistance to some populations, does not have to be considered, because S. nigrum seldom occurs in Scottish fields.

In the Appendix 2, evidence is presented that pathotype B is recessive to pathotype A and is also weaker or less fit than pathotype A in ordinary reproduction in potato varieties lacking all resistance genes.

Pathotype B was much less frequent than pathotype A in the fields which were investigated and was detected in smaller or larger patches within infestations. The patches were found mainly in areas of low population density.

These observations can be reconciled as follows:

It is suggested that patches of pathotype B arose through founder effect, and were initially distributed at random. With

increase in population density and continuous spread, patches of pathotype B began to coalesce with patches of pathotype A. The frequency of pathotype B in the merging patches then declined to a low and almost undetectable level due to introgression of the dominant allele conferring specificity A, coupled with the fitness advantage of pathotype A, so that only a few newer, well isolated patches of pathotype B could be evident at any time, mainly in the less densely infested areas.

If this sequence of events were to continue, specificity B would be reduced eventually to a very low frequency, such as would be maintained by recurrent mutation.

The present frequency of pathotype B in Britain or European populations is very obscure, because until recently, pathotype B was not distinguished from pathotype E, which now seems much more common than pathotype B, especially in the North of England.

However, pathotype E did not occur in the fields which were investigated and pathotype B, the recessive homozygote was certainly not rare in any of them; its frequency varied from 1/423 to 1/10 (Table 3.10), with a mean of 1/55 $\pm$ 29, commensurate with a mean frequency of vb in the region of 1/7·5 $\pm$ 5·4. This is very high frequency for a gene which is disadvantageous when homozygous, c.f. 1/141 for the recessive gene determining albinism in human populations (Stern, 1949). Disadvantageous genes are nearly always recessive.

It was calculated that vb was heterozygous in or carried by

1 in 4·3 ± 0·63 of the females which matured in the combined S2 generation from all fields which were investigated. The heterozygotes varied in frequency from 1 in 2·3 to 1 in 10·8 in the different fields.

It is a generally accepted proposition that if a gene which is disadvantageous when homozygous is maintained at a greater frequency than can be maintained by recurrent mutation, it must have some compensating heterozygous advantage. The combination of allelomorphy with heterozygous advantage is the most common basis for balanced genetic polymorphism in a population. Ford (1940) defined genetic polymorphism as "the occurrence together in the same habitat of two or more discontinuous forms, of "phases", of a species in such proportions that the rarest of them cannot be maintained merely by recurrent mutation". He also stated (Ford, 1965) that "a unifactorial character must be polymorphic if found even in 1 per cent of a considerable population, amounting perhaps to 500 individuals or more, when random genetic drift may reasonably be excluded as unimportant". This statement obviously refers to populations in Hardy-Weinberg equilibrium, and not to populations in which genetic readjustment is taking place, following the merging of two genetically distinct populations which will produce a transient polymorphism but not necessarily a permanent polymorphism.

It is necessary to consider which was the more likely in the fields investigated, a transient polymorphism or a permanent polymorphism. If transient, it has to be assumed that populations of

pathotype A and pathotype B may exist separately and were merging in the fields which were investigated.

There is no evidence that populations of pathotype B exist and Guile (personal communication) maintains that pathotype B is rare by comparison with E and A and that no pure population of pathotype B has been found. The best known pathotype B population is probably the Duddingston population but this was produced by generations of selection through varieties having the resistance of subsp. andigena. Furthermore, it was concluded from the investigations of population density (Section 1) that the nematode infestations had derived mainly from a very small number of founder cysts and that many generations had passed in the build up of infestations to their present levels. Therefore there is no reason to suppose that these populations were seriously out of equilibrium. It is suggested that their variability exemplified permanent genetic polymorphism. It is also suggested that when the balance between pathotype A and B is temporarily disturbed as a result of founder effect in field populations it will tend to be restored in time.

The significance of balanced polymorphism in potato cyst nematode.

The rate of change in populations of a parasite due to selection pressure resulting from the cultivation of a resistant host can be influenced by so many factors that any comprehensive, mathematical treatment of the subject is bound to be complicated. In order to assess the importance of the various factors affecting the breakdown of resistance to potato cyst nematode,

Jones *et al.* (1967) first wrote out a computer programme incorporating laws governing multiplication rates, inheritance of specificity, and change in the sex ratio, and proceeded to predict the population changes to be expected, under a range of conditions, if resistant and susceptible varieties were to be grown continuously or alternatively in certain cycles.

They concluded that reproductive rate was relatively unimportant as a determinant of genetic change, meaning change within the limits imposed by a model genetic system. Since the genetic system arrived at in the course of evolution is likely to be the one best suited to a parasite's productive rate it could be argued that reproductive rate determines not so much change according to any particular system, but the system itself.

Potato cyst nematode clearly has a very low reproductive rate as compared with parasitic fungi such as *Phytophthora infestans* and *Puccina striiformis*, which produce an abundance of air-borne spores by asexual means; a single mutant spore of either fungus could probably initiate breakdown of resistance on an epidemic scale. In view of its low reproductive rate *H. rostochiensis* might almost be expected to possess a sophisticated genetic system governing resistance breaking. It is suggested that balanced polymorphism of the specificity genes Va and vb in *H. rostochiensis* compensates for its low reproductive rate, in that a certain balance between these alleles is brought about by the increased fitness of the heterozygotes. As a result, even the gene vb which is apparently disadvantageous when homozygous could

be maintained indefinitely in a population multiplying on fully susceptible varieties such as Craigs Defiance, and at a frequency higher than could be achieved by mutation. The significance of this will be evident by the fact that Jones et al. (1967) established that the initial frequency of resistance-breaking biotypes in a population was one of the factors which were important determinants of genetic change leading to the breakdown of resistance.

In passing, it is worth noting that resistance-breaking biotypes multiplying in plants incorporating the corresponding resistance gene are not likely to become fixed for specificity, since males in any generation need not possess the resistance-breaking character. A balance between specificity alleles might still be maintained in this way.

Ford (1965) gives many instances of polymorphism involving genes which appear to be disadvantageous when homozygous and which owe their persistence to the increased fitness of the heterozygotes incorporating them.

This is the essence of ecological genetics, the fact that genetic polymorphism maintains a level of variability such that organisms can respond quickly to changes in their environment. It is suggested that it allows the potato cyst nematode to respond quickly to changes in the direction of resistance in its host, a coevolutionary process of 'keeping in step' and an adaptation to parasitism in the broadest sense.

Index to Field Maps

Map 1a.

Field: Burnside, O.S. Number,[1] 0005.

Location: Sea Cliff, North Berwick, East Lothian.

Area: 28·17 acres.

Soil type and drainage:[2] Raised beach, sand and gravel, freely drained.

Height above sea level: 100 feet approximately.

Cropping history: 1960-61 Cabbage and Beetroot.
1961-62 Peas, Broccoli and Brussel Sprouts.
1962-63 Swedes, Beetroot and Barley.
1963-64 Early Potatoes, Broccoli and Cabbages.
1964-65 Cabbages, Beetroot and Leeks.

Date of soil sampling: November, 1964.

Spacing between sampling points: 20 x 20 yards for the first four acres on the east side of the field and 30 x 30 for the remaining area.

Total number of soil samples collected: 165.

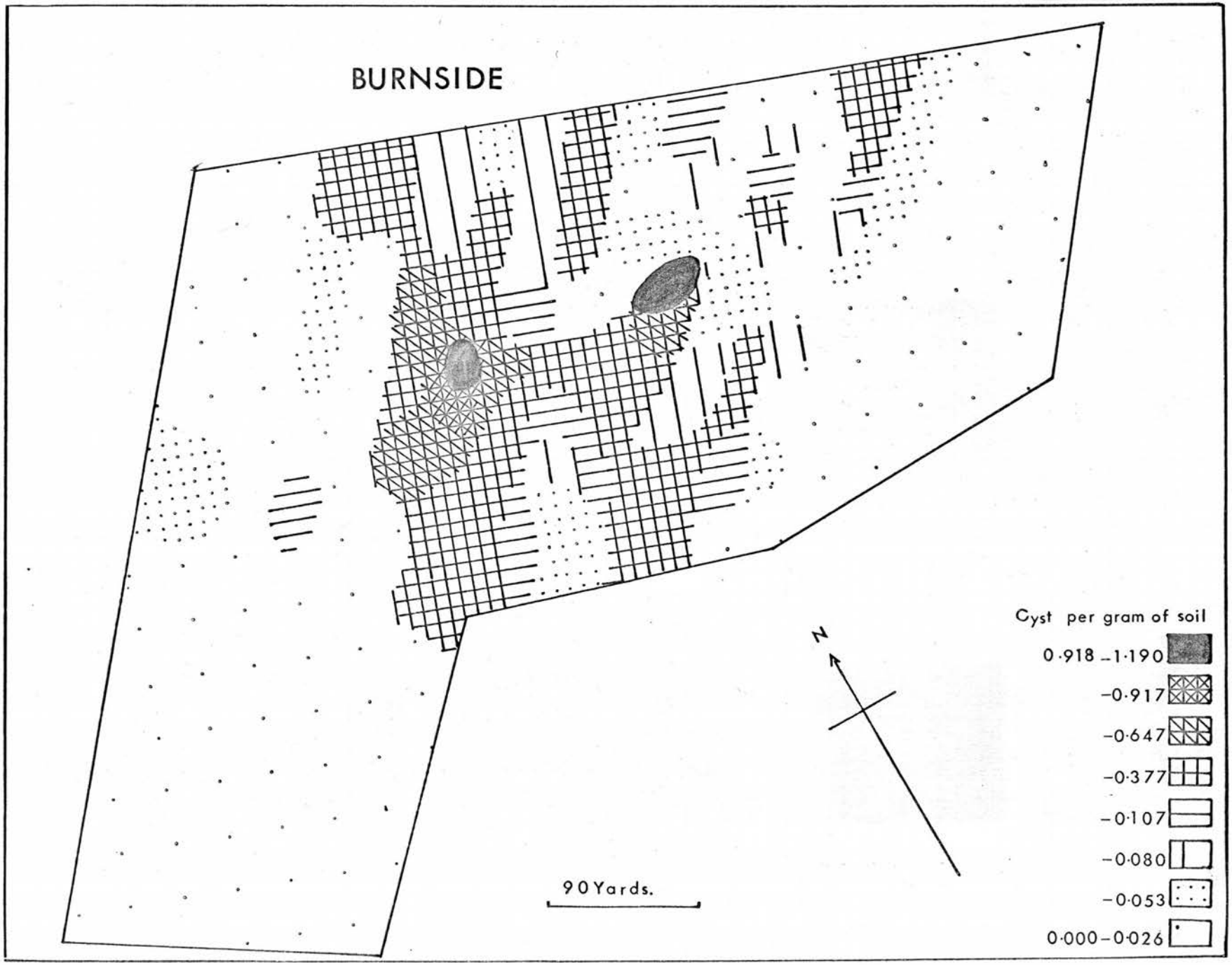
Average cyst density for the field: 0·107 cysts per gm. air-dried soil.

1. Ordnance Survey map, 1:25000, sheet No. NT 6183. Revised edit. 1965.

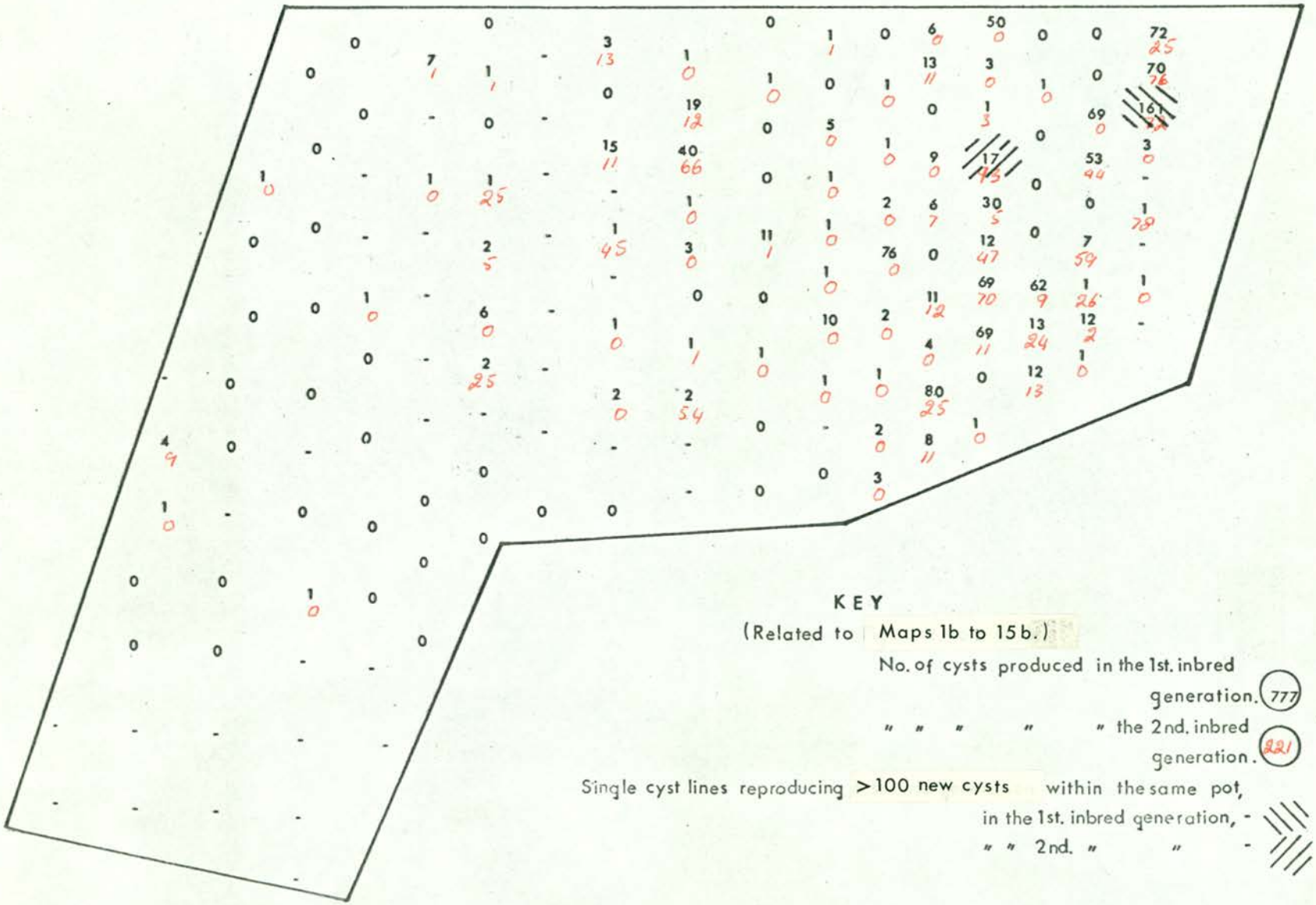
2. Soil survey of Scotland, 1966.

Observations: The infestation is more or less confined to the central third of the field, which probably reflects the fact that in most years the field has supported three different crops, and the infested area may have been used most often for growing potatoes. A potato crop had been lifted from this part of the field in early 1964. The infestation is patchy, showing two foci of infestation, with a zone of continuous spread surrounding one and a notably steep decline in infestation northwards of the other. It appears that infested zones associated with the two foci are beginning to merge. Even in the infested third, the level of infestation is low and there would appear to be scope for further spread and increase of infestation. The field is exposed to strong winds, particularly from the North.

MAP 1,a.


BURNSIDE
N
90 Yards.
Cyst per gram of soil
0·918 – 1·190
– 0·917
– 0·647
– 0·377
– 0·107
– 0·080
– 0·053
0·000 – 0·026

BURNSIDE



KEY

(Related to Maps 1b to 15b.)

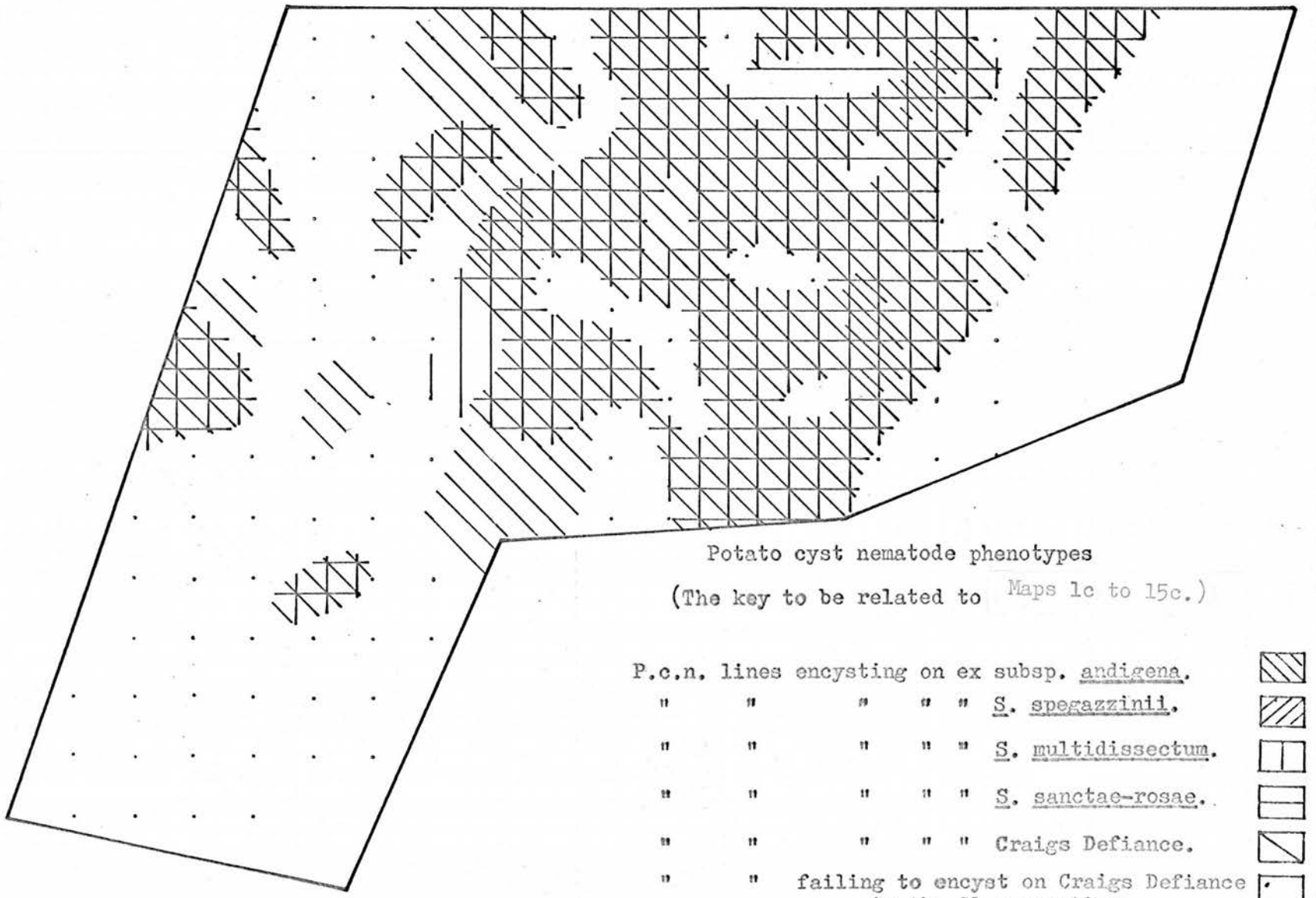
No. of cysts produced in the 1st. inbred generation. (777)

" " " " " the 2nd. inbred generation. (221)

Single cyst lines reproducing >100 new cysts within the same pot, in the 1st. inbred generation, -

" " 2nd. " " -

BURNSIDE


Potato cyst nematode phenotypes
(The key to be related to Maps 1c to 15c.)
P.c.n. lines encysting on ex subsp. andigena.
" " " " " S. spegazzinii.
" " " " " S. multidissectum.
" " " " " S. sanctae-rosae.
" " " " " Craigs Defiance.
" " failing to encyst on Craigs Defiance in the S1 generation.

Field: Burnside

Population grid intersection number	Number of cysts recovered in the parent population	Total number of cysts produced on Craigs S1 generation	Defiance S2 generation	H1 ex adg	Fa ex spg	H2 ex mlt	H2 ex sct	H1H2 adg x mlt	H1H2 adg x sct
1	2	3	4	5	6	7	8	9	10
1	6	72	25	2	-	12	52	0	0
2	6	70	76	0	-	26	7	-	-
3	8	161	72	0	-	45	66	-	-
4	4	3	0	0	-				
5	0	-		0	-				
6	5	1	78	0		9	0		
7	0	-							
8	0	-							
9	0	-							
10	0	-							
11	4	1	2	0					
12	4	11	26	0	-	17	10	-	-
13	6	1	59						
14	4	7	0	0	-	1	-		
15	13	0	-						
16	27	53	44	0	-	4	20	-	-
17	44	69	0	0	-				
18	6	0							
19	38	0							
20	5	0							
21	5	1	0	0					
22	1	0							
23	1	0							
24	3	0							
25	8	0							
26	17	62	9	0	-	10	83	-	-
27	6	13	24	1	-	-	35	0	0
28	2	0	-						
29	14	12	13	0	-	1	25	-	-
30	31	1	0						
31	25	0	-						
32	34	69	11	0	-	22	44	-	-
33	66	69	70	0	-	33	33	-	-
34	39	12	47	1	-	18	17	0	0
35	16	30	5	0	-	3	16	-	-
36	18	17	93	0	-	3	29	-	-
37	60	1	3						
38	28	3	0	0	-				
39	22	50	0	2	-	8	19	0	0
40	4	6	0	0	-	6	24	-	-

Field: Burnside (Contd)

1	2	3	4	5	6	7	8	9	10
41	2	13	11	0	-	6	5	-	-
42	7	0	-						
43	15	9	0	0	-	18	-		
44	9	6	7			16	39	-	-
45	12	0	-						
46	21	11	12	0	-	1	30	-	-
47	24	4	0	0	-	8	4		
48	75	80	25	0	-	25	7	-	-
49	97	8	11	0	-	6	32	-	-
50	45	3	0	0		2	34		
51	40	2	0	0	-				
52	22	1	0	0	-				
53	63	2	0	0	-				
54	157	76	0	0	-	9	13	-	-
55	357	2	0						
56	16	1	0			-	23		
57	18	1	0						
58	76	0	-			-	47		
59	7	1	1	0					
60	2	0	-						
61	15	5	0	-	-	1	0		
62	3	1	0						
63	49	1	0	-	-				
64	51	1	0						
65	70	10	10	0	-	16	13		
66	26	1	0	-					
67	14	0	-						
68	25	0	-						
69	12	0	-						
70	20	1	0						
71	35	0	-						
72	55	11	1		-	1	3	-	-
73	17	0	-						
74	78	0	-						
75	88	1	0						
76	72	0	-						
77	32	1	0	0					
78	28	19	12	0	-	62	13	-	-
79	26	40	66	-	-	14	7	-	-
80	37	1	0						
81	183	3	0	-		-	1		
82	152	0	-						
83	71	1	1						
84	76	2	54	0		5	-		
85	81	0	-						
86	123	0	-						

Field: Burnside (Contd.)

1	2	3	4	5	6	7	8	9	10
87	111	0	-						
88	56	2	0						
89	179	1	0						
90	198	1	45	0					
91	278	0	-						
92	90	15	11	-	-	20	25	-	-
93	108	0	-			6	31		
94	157	0	-						
95	11	3	13	0	-	15	-		
96	25	0	-						
97	22	1	1						
98	245	0	-						
99	170	1	25	1		2	-		
100	112	2	5	-	-	39	-		
101	178	6	0	-	-	-	-	-	
102	166	2	25	0	-	7	-		
103	3	0	-						
104	2	0	-						
105	2	0	-						
106	0								
107	0								
108	2	0	-						
109	1	0	-						
110	6	0	-						
111	7	0							
112	95	7	1	-	-	32	21	-	-
113	48	0	-						
114	12	0	-						
115	11	1	0						
116	16	1	0						
117	0								
118	1	0	-						
119	26	0	-						
120	0								
121	1	0	-						
122	1	0	-						
123	0								
124	0								
125	0								
126	0								
127	0	-							
128	0	-							
129	4	1	0						
130	0	-							
131	0	-							
132	14	4	9	-	-	79	32		

Field: Burnside (Contd.)

1	2	3	4	5	6	7	8	9	10
133	4	0	-						
134	7	1	0						
135	2	0							
136	0	-							
137	5	0							
138	0	-							
139	0	-							
140	0	-							
141	0	-							
142	2	0							
143	0	-							
144	4	0							
145	1	0							
146	1	0							
147	0	-							
148	5	1	0	0	-				
149	7	0							
150	3	0							
151	11	0							
152	0	-							
153	0	-							
154	0	-							
155	0	-							
156	0	-							
157	0	-							
158	0	-							
159	0	-							
160	0	-							
161	0	-							
162	0	-							
163	0	-							
164	0	-							
165	0	-							
Means	0·107	5·23	13·3	0·22	-	13·85		24·94	- -
Maximum	1·190	161	93	2	-	79		83	- -
Minimum	0·026	0	0	0	-	1		0	- -

Map 2a.

Field: Barebanes, O.S. Number,[1] 8525.

Location: Loch-house, North Berwick, East Lothian.

Area: 14·61 acres.

Soil type and drainage:[2] Raised beach, silts and clays. Imperfectly drained.

Height above sea level: 200 feet approximately.

Cropping history: 1960-61 Carrots and Wheat.
1961-62 Sugarbeet and Mangolds.
1962-63 Wheat.
1963-64 Barley.
1964-65 Early Potatoes followed by Wheat.

Date of soil sampling: November, 1964.

Spacing between sampling points: 30 x 30 yards.

Total number of soil samples collected: 63.

Average cyst density for the field: 0·704 cysts per gm. air-dried soil.

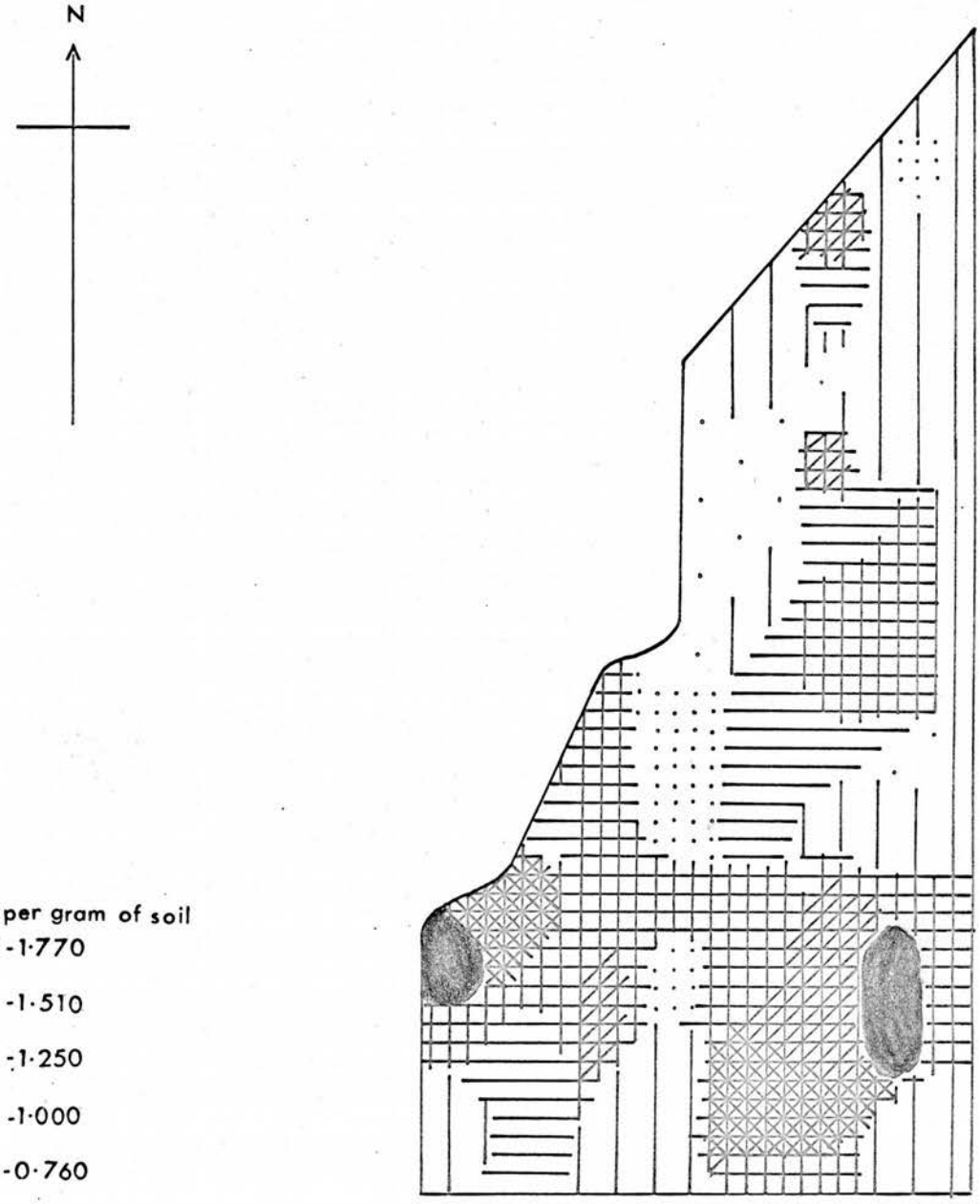
1. Ordnance survey map, 1:25000, sheet No. NT 6181. Revised edit. 1965.

2. Soils survey of Scotland, 1966.

Observations: There appear to be two principal foci of infestation both surrounded by zones of more or less continuous spread, which are beginning to merge. Secondary and tertiary foci lie to the north of one of the primary foci, giving the impression that the infestation is spreading mostly in this direction, probably due to the fact that the field is usually cultivated in this direction. There seems to be considerable scope for further spread and increase in the level of infestation particularly towards the northern region of the field.

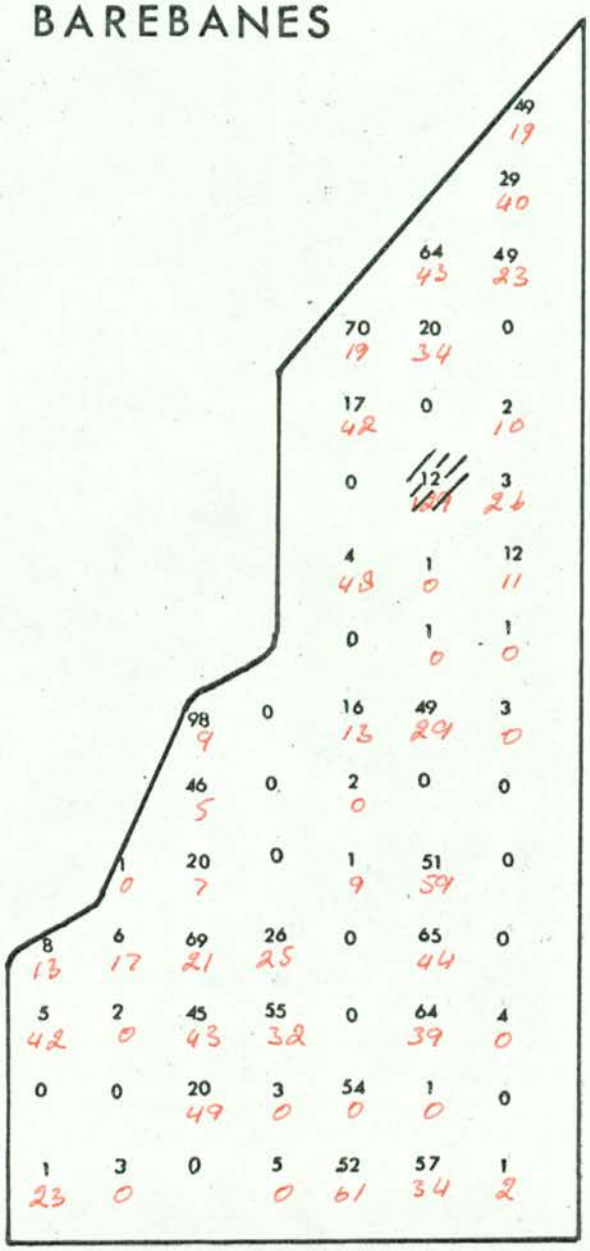
MAP 2, a.

BARE BANES



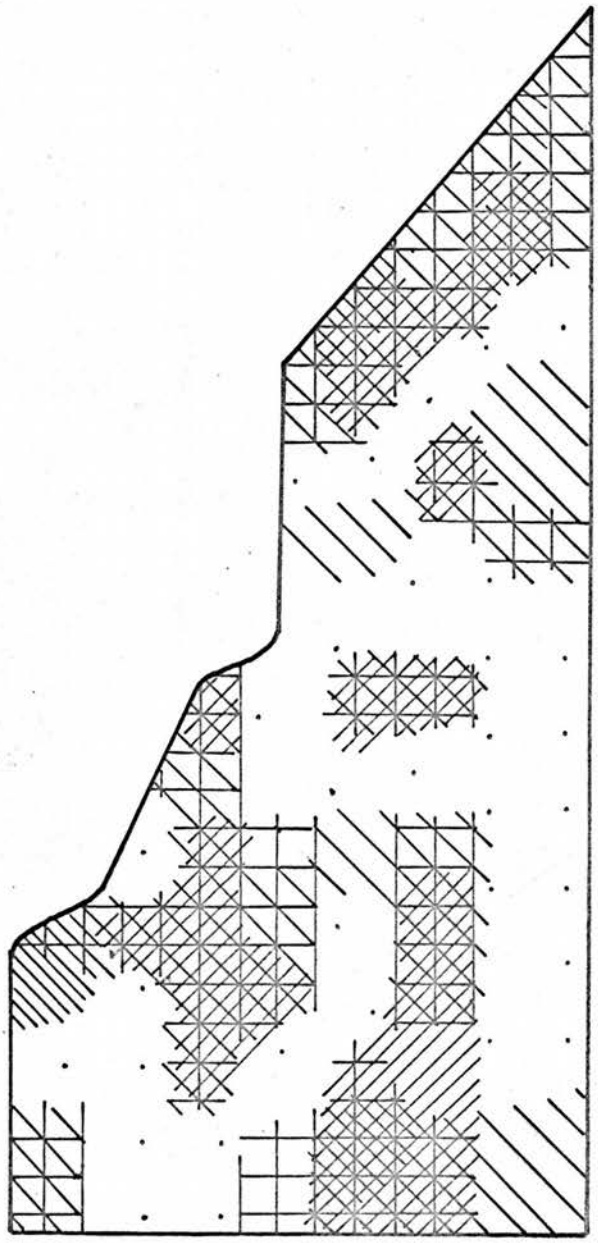
MAP 2,b.

BAREBANES



MAP 2,c.

BAREBANES



Field: Barebanes

Population grid intersection number	Number of cysts recovered in the parent population	Craigs S1 generation	Total number of cysts produced on Defiance S2 generation	H1 ex adg	Fa ex spg	H2 ex mlt	H2 ex sct	H1H2 adg x mlt	H1H2 adg x sct
1	2	3	4	5	6	7	8	9	10
1	66	1	2						
2	268	0	-						
3	315	4	0	-	-				
4	122	0	-						
5	59	0	-						
6	26	0	-						
7	133	3	0	0		8			
8	122	1	0						
9	127	12	11	0	0	10	13	-	-
10	62	3	26	0	-	44			
11	76	2	10	0	-				
12	74	0	-						
13	76	49	23	1	1	43	48	0	0
14	33	29	40	0	1	16	6	0	0
15	62	49	19	2	0	1	71	0	0
16	184	64	43	0	0	29	51	-	-
17	102	20	34	0	1	11	85	-	-
18	25	0	-						
19	183	12	124	0	3	10	7	0	0
20	110	1	0						
21	151	1	0						
22	131	49	29	0	1	3	15	0	0
23	94	0	-						
24	73	51	59	0	0	15	41	-	-
25	249	65	44	0	1	64	39	0	0
26	192	64	39	0	3	30	35	0	0
27	171	1	0	0	1	39			
28	201	57	34	0	2	27	6	0	0
29	196	52	61	1	4	29	29	0	0
30	208	54	0	0	2	29	14	0	0
31	135	0	-						
32	129	0	-						
33	108	1	9	0		21			
34	178	2	0	0					
35	195	16	13	0	2	29	61	0	0
36	144	0	-						
37	44	4	48	0		17			
38	56	0	-						

Field: Barebanes (Contd.)

1	2	3	4	5	6	7	8	9	10
39	168	17	42	0	1	8	44	0	0
40	136	70	19	1	1	46	78	0	0
41	28	0	-						
42	34	0	-						
43	46	0	-	0	0	18	11	-	
44	131	26	25	0	0	32	7	-	-
45	40	55	32	0	3	10	40	0	0
46	83	3	0						
47	132	5	0	0	0	1	2	-	
48	118	0	-						
49	349	20	49	0	1	9	29	-	-
50	356	45	43	0	2	19	19	0	0
51	257	69	21	0	1	14	51	-	-
52	288	20	7	0	1	15	34	-	-
53	270	46	5	0	0	11	28	-	-
54	254	98	9	0	1	12	20	-	-
55	220	1	0						
56	415	6	17	0	1	9	4	-	-
57	276	2	0	0					
58	198	0	-						
59	210	3	0	2	0	2			
60	148	1	23	0	0	1	29	-	-
61	297	0	-						
62	319	5	42	1	0	2	0	-	-
63	236	8	13	3	0	45	4	-	-
Means	0·704	18·5	22·6	0·30	1·15	21·96	28·29	-	-
Maximum	2·126	98	124	2	4	64	85	-	-
Minimum	0·093	0	0	0	0	1	0	-	-

Map 3a.

Field: Spittal, O.S. Number,[1] 0036.

Location: Spittal, Longniddry, East Lothian.

Area: 34 acres.

Soil type and drainage:[2] Till derived from carboniferous sediment. Imperfectly drained.

Height above sea level: 250 feet approximately.

Cropping history: 1960-61 Barley.
1961-62 Swedes.
1962-63 Barley.
1963-64 Potatoes.
1964-65 Wheat.

Date of soil sampling: December 1964.

Spacing between sampling points: 30 x 30 yards.

Total number of soil samples collected: 172.

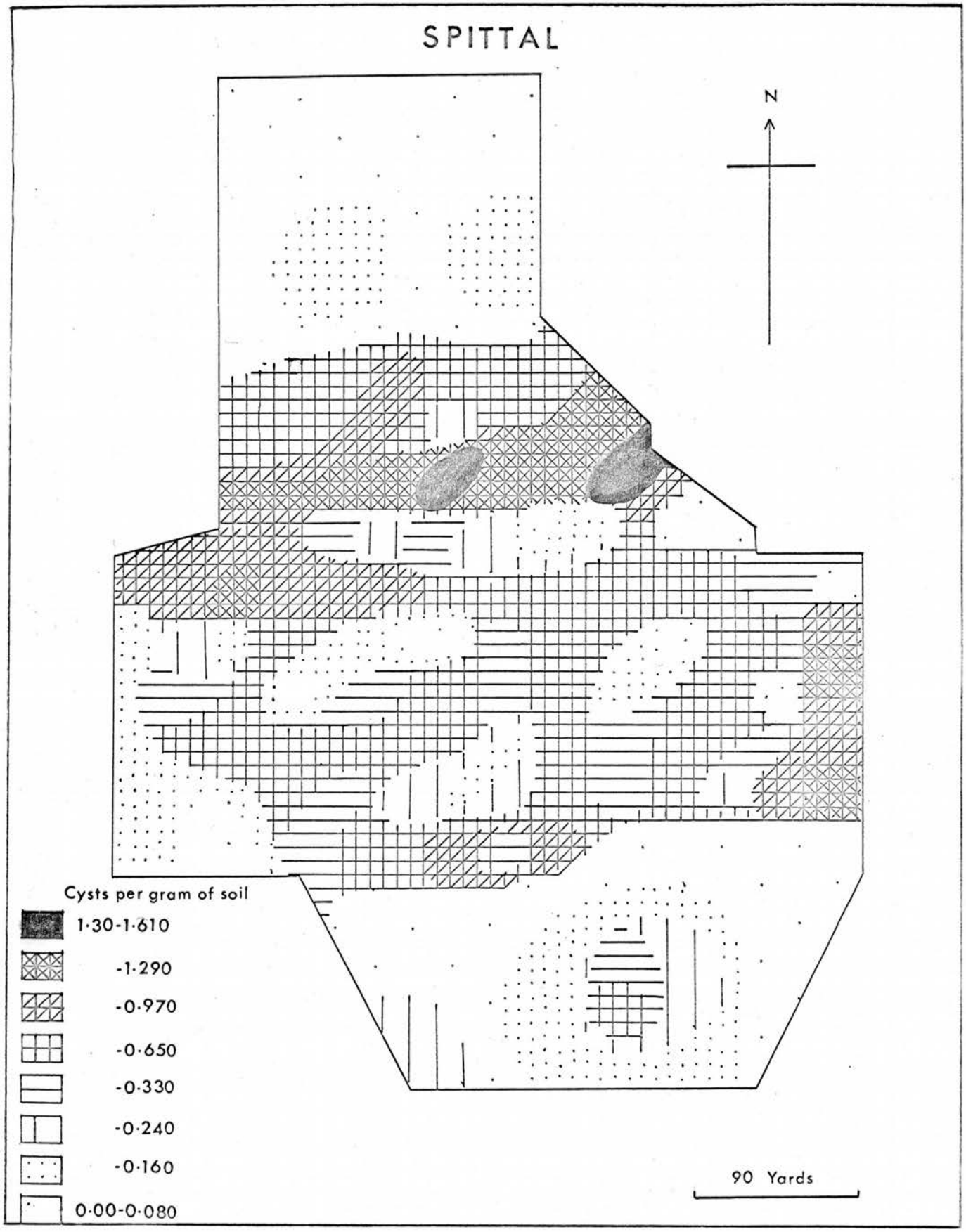
Average cyst density for the field: 0·335 cysts per gm. of air-dried soil.

1. Ordnance survey map, 1:25000, sheet No. NT 4677. Revised edit. 1965.

2. Soil survey of Scotland, 1966.

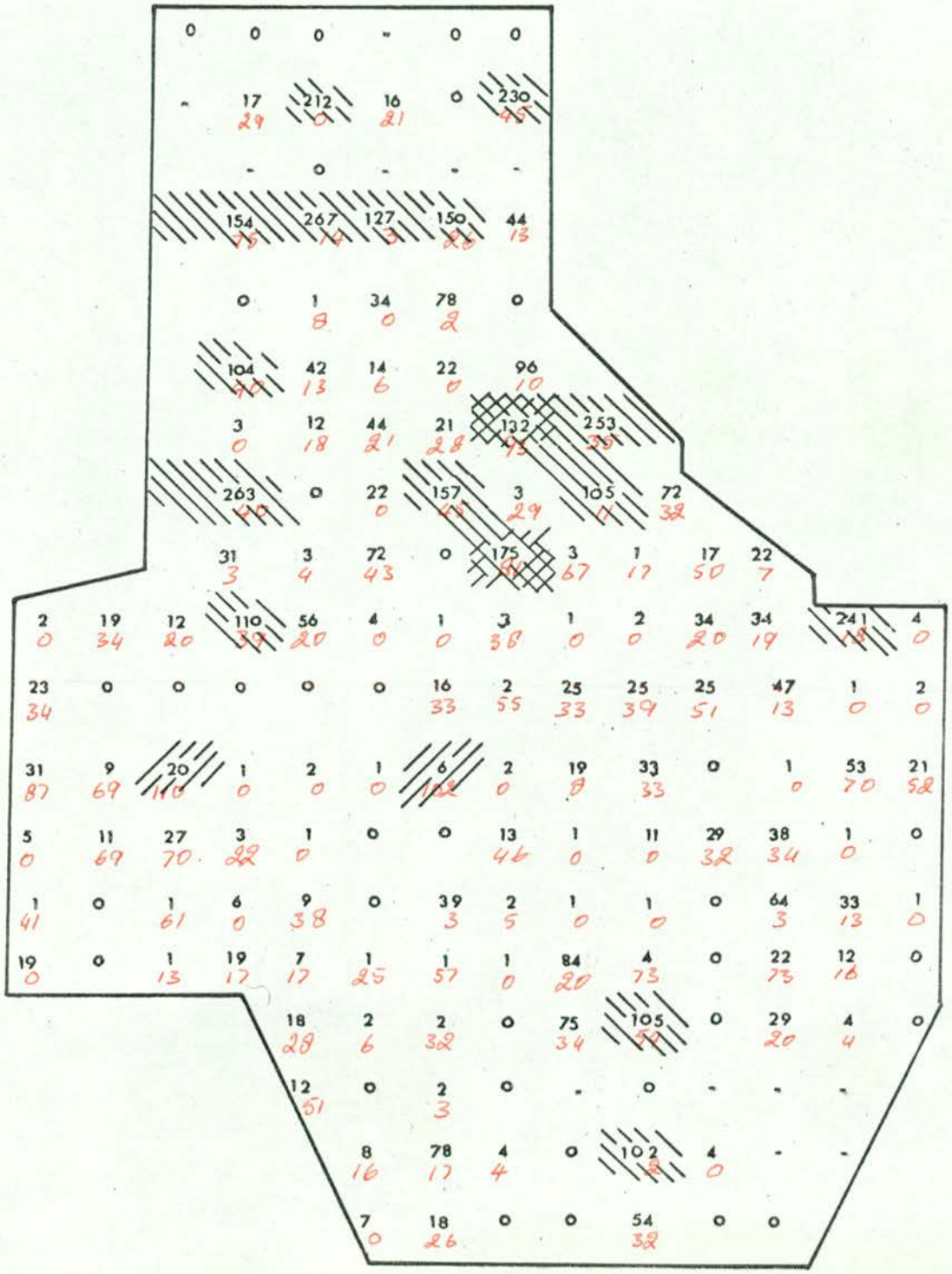
Observations: Since 1960 this field has been cropped as a unit although the rather sharp delimitation of the infested area, and also its shape and position, suggest that the central area may have been cropped more often by potatoes at some earlier period. There appear to be two foci or possibly one main centre of infestation from which continuous spread has proceeded mainly in an east/west direction. There is a well marked second focus near the eastern boundary and evidence of later foci elsewhere in the lightly infested regions. One of these is developing near the southern boundary, which lies on a north/south slope in which direction spread seems to be taking place from the focus. There appears to be considerable scope for further spread and increase in infestation.

MAP 3,a.

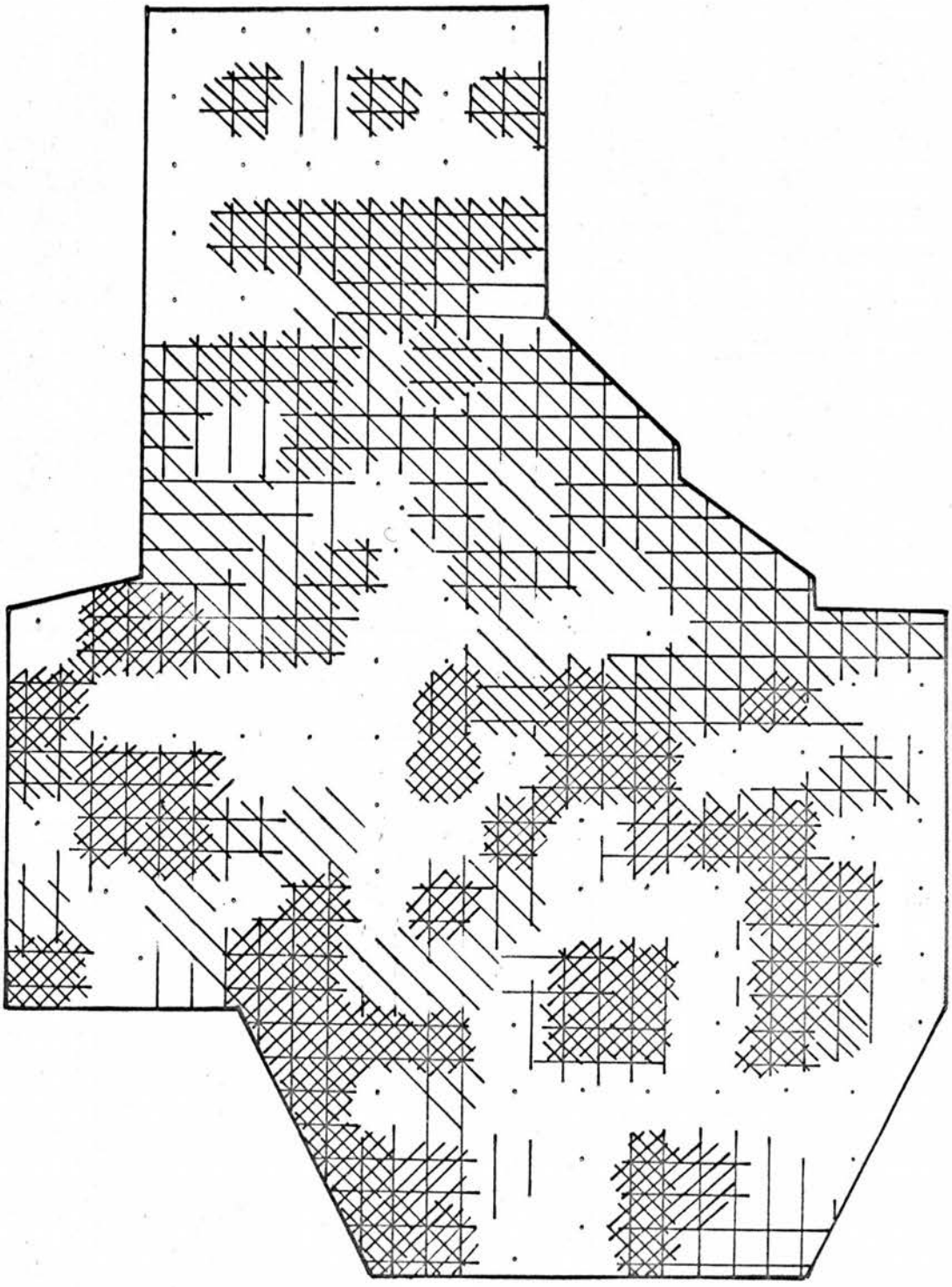

SPITTAL
N
Cysts per gram of soil
1·30-1·610
-1·290
-0·970
-0·650
-0·330
-0·240
-0·160
0·00-0·080
90 Yards

MAP 3,b.

SPITTAL



SPITTAL



Field: Spittal

Population grid intersection number	Number of cysts recovered in the parent population	Total number of cysts produced on Craigs S1 generation	Defiance S2 generation	H1 ex adg	Fa ex spg	H2 ex mlt	H2 ex sct	H1H2 adg x mlt	H1H2 adg x sct
1	2	3	4	5	6	7	8	9	10
1	2	0							
2	2	0							
3	3	0							
4	0								
5	2	0							
6	5	0							
7	3	230	45	1	-	19	67	0	0
8	5	0							
9	6	16	21	4	-	43	39	0	0
10	19	212	0	0	-	40			
11	4	17	29	35	-	47	64	0	0
12	0								
13	0								
14	1	0							
15	0								
16	0								
17	0								
18	45	44	13	7	-	68	61	0	0
19	14	150	26	1	-	16	11	0	
20	17	127	3	1	-	9	7	0	0
21	26	267	14	1	-	7	19	0	0
22	3	154	75	1	-	4	18	0	0
23	2	0							
24	12	1	8	0					
25	15	34	0	1	-	4	57	0	0
26	31	78	2	0	-	8	14	-	-
27	1	0							
28	265	96	10	0	-	17	54	-	-
29	140	22	0	1	-	0	2	0	0
30	284	14	6	0	-	17	0	-	-
31	246	42	13	1	-	4	33	0	0
32	138	104	40	2	-	17	40	0	0
33	49	3	0	0	-	1			
34	166	12	18	1	-	2	8	0	0
35	262	44	21	0	-	29	10	-	-
36	77	21	28	0	-	17	25	-	
37	17	132	93	0	-	56	5	-	
38	510	253	35	0	-	65	7	-	-

Field: Spittal (Contd.)

1	2	3	4	5	6	7	8	9	10
39	652	72	32	0	-	13	19	-	-
40	415	105	11	0	-	21	24	-	-
41	504	3	29	0	-	12			
42	560	157	45	0	-	7	22	-	-
43	493	22		0					
44	512	95		-	-	3	69	-	-
45	497	263	40	0	-	0	4	-	-
46	389	31	3	0	-	0	8	-	-
47	400	3	4	-		5			
48	78	72	43	1	-	8	26	0	0
49	129	14		0					
50	80	175	81	1	-	52	46	0	0
51	19	3	67	-	-	38	48	-	-
52	47	1	17	0					
53	16	17	50	0	-	35	43	-	-
54	15	22	7	0	-	21	16	-	-
55	1	4		-	-	13	80	-	
56	126	241	18	0	-	45	27	-	-
57	244	34	19	0	-	1	18	-	-
58	132	34	20	0	-	40	18	-	-
59	142	2							
60	168	1							
61	139	3	38	0		2			
62	172	1	0						
63	321	4	0						
64	274	56	20	1	0	8	4	0	-
65	319	110	39	0	0	6	11	-	-
66	408	12	20	0	1	7	1	-	-
67	258	19	34	1	1	23	3	0	-
68	157	2	0						
69	51	23	34	1	1	19	2	0	-
70	72	0	-						
71	101	0	-						
72	402	0	-						
73	72	0	-						
74	24	0	-						
75	30	16	33	1	2	6	0	0	-
76	112	2	55	2	0		3		
77	279	25	33	1	2	10	7	0	-
78	263	25	39	1	0	6	2	0	-
79	39	25	51	0	0	10	13	0	-
80	310	47	13	2	1	10	6	0	-
81	220	1	0						
82	333	2	0						
83	404	21	53	0	0	82	0	-	-
84	119	53	70	0	0	40	79	-	-

Field: Spittal (Contd.)

1	2	3	4	5	6	7	8	9	10
85	277	1	0						
86	285	0	-						
87	55	33	33	1	3	34	36	0	-
88	348	19	8	1	1	52	23	0	-
89	174	2	0						
90	373	6	102	2	6				
91	245	1	0						
92	173	2	0						
93	17	1	0						
94	227	20	119	0	1	25	61	0	-
95	96	9	69	0	1	48	25	0	-
96	169	31	87	2	0	60	29	0	-
97	42	5	0						
98	416	11	69	0	1	34	52	0	-
99	242	27	70	3	1	21	86	0	-
100	151	3	22	0	0	62	67	-	-
101	323	1	0						
102	302	0	-						
103	355	0	-						
104	48	13	46	1	1	48	28	0	-
105	287	1	0						
106	224	11	0	0	7	112	13	0	-
107	195	29	32	1	1	52	88	0	-
108	238	38	24	1	1	42	48	0	-
109	57	1	0						
110	373	0	-						
111	503	1	0						
112	212	33	18	0	1	32	40	-	-
113	68	64	3	1	6	47	40	0	-
114	250	0	-						
115	154	1	0						
116	102	1	0						
117	88	2	3	0		2			
118	42	39	5	0	1	25	37	-	-
119	82	0	-						
120	111	9	38	2	5	36	37	0	- -
121	209	6	0	0					
122	37	1	61	0		5			
123	31	0							
124	35	1	41	0		14			
125	55	19	0	1	1	40	66	0	
126	78	0	0						
127	16	1	13	0		0			
128	105	19	17	0	5	30	98	0	-
129	222	7	17	1	1	36	66	0	-
130	183	1	25	0		1			

Field: Spittal (Contd.)

1	2	3	4	5	6	7	8	9	10
131	266	1	57	0		43			
132	102	1							
133	269	84	20	0	1	33	18	0	-
134	14	4	73	1	1	78			
135	4	0							
136	7	27	73	1	2	44	37	0	-
137	15	12	16	0	1	33	35	-	-
138	6	0							
139	9	0							
140	0			0		29			
141	11	29	20	1	2	100	48	0	-
142	3	0							
143	13	105	54	2	2	39	54	0	-
144	19	75	34	1	4	23	66	0	-
145	3	0							
146	3	2	32	1	1	32	20	0	-
147	2	2	6	3					
148	3	18	28	0	2	13	63	-	-
149	7	12	51	1	2	44	25	0	-
150	4	0							
151	24	2	3	0		5			
152	10	0							
153	2	0							
154	130	0							
155	0								
156	0								
157	0								
158	0								
159	0								
160	96	4	0	0	4	50	62		
161	171	102	2	5	0	60	32	0	-
162	56	0							
163	53	4	4	0		14			
164	21	78	17	0	1	11	27	0	-
165	27	8	16	1	2	25	34	0	-
166	76	7	0	3	1	60	41	0	-
167	9	18	26	0	1	19	29	0	-
168	5	0							
169	6	0							
170	2	54	32	6	4	22	17	0	-
171	2	0							
172	10	0							
Means	0·335	30·6	26·3	0·82	1·57	23·96	32·61	-	-
Maximum	1·625	267	119	35	7	100	98	-	-
Minimum	0·00	0	0	0	0	0	0	-	-

Map 4a.

Field: Archerfield 14, O.S. Number,[1] 4000.

Location: Archerfield, Dirleton, East Lothian.

Area: 12·78 acres.

Soil type and drainage:[2] Till derived from lower carboniferous sediment and igneous rock. Freely drained.

Height above sea level: 150 feet approximately.

Cropping history:

1960-61	Early Potatoes
1961-62	Wheat.
1962-63	Fallow.
1963-64	Early Potatoes.
1964-65	Wheat.

Date of soil sampling: December, 1964.

Spacing between sampling points: 30 x 30 yards.

Total number of soil samples collected: 60.

Average cyst density for the field: 0·127 cysts per gm. air-dried soil.

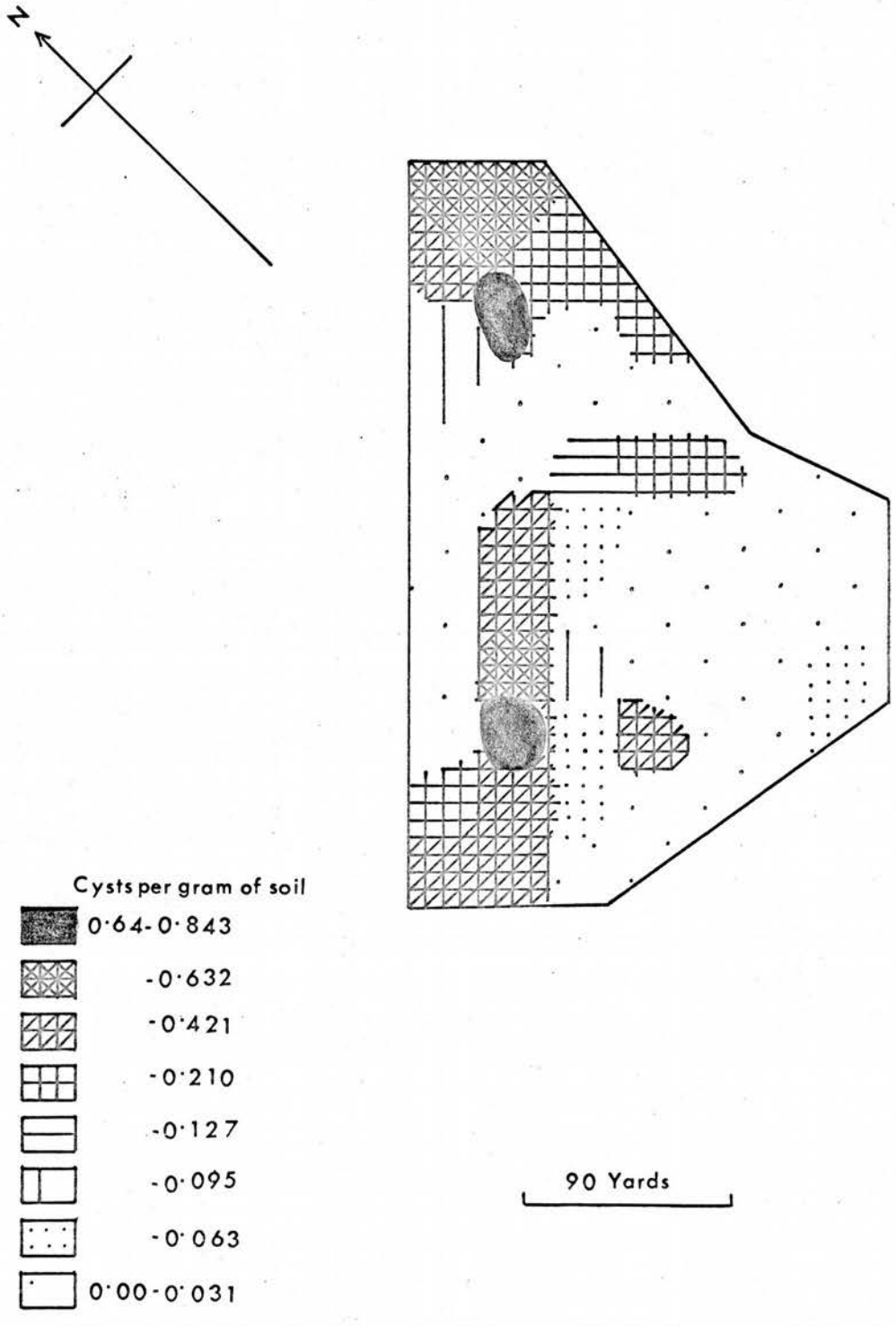
1. Ordnance survey map, 1:25000, sheet No. NT 5083. Revised edit. 1965.

2. Soil survey of Scotland, 1966.

Observations: There appear to be two foci of infestation which are of comparable age, both surrounded by zones of continuous spread. Most spread is in a north/south direction, the direction in which the field is usually cultivated. There are also one or two outlying, apparently younger, foci of infestation. The level of cyst density in the most heavily infested area of the field is still quite low, there is thus considerable scope for further spread and increase in infestation.

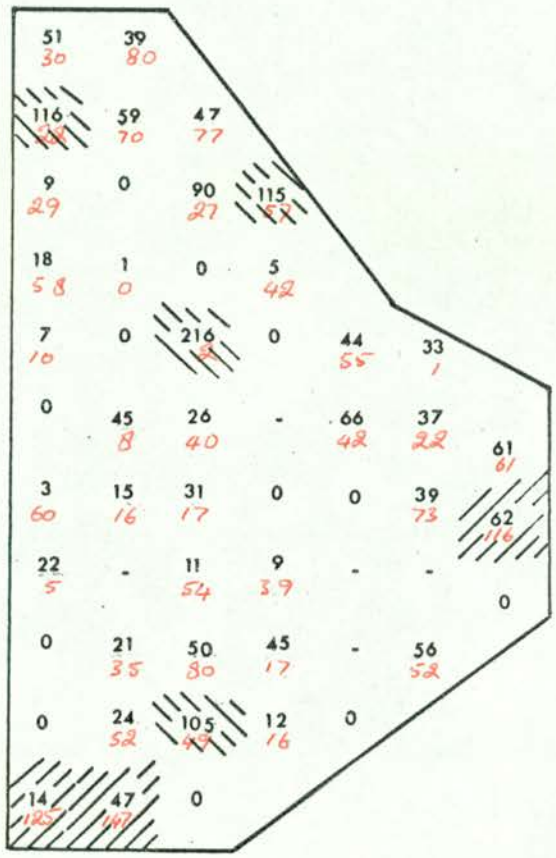
MAP 4,a.

ARCHERFIELD–14



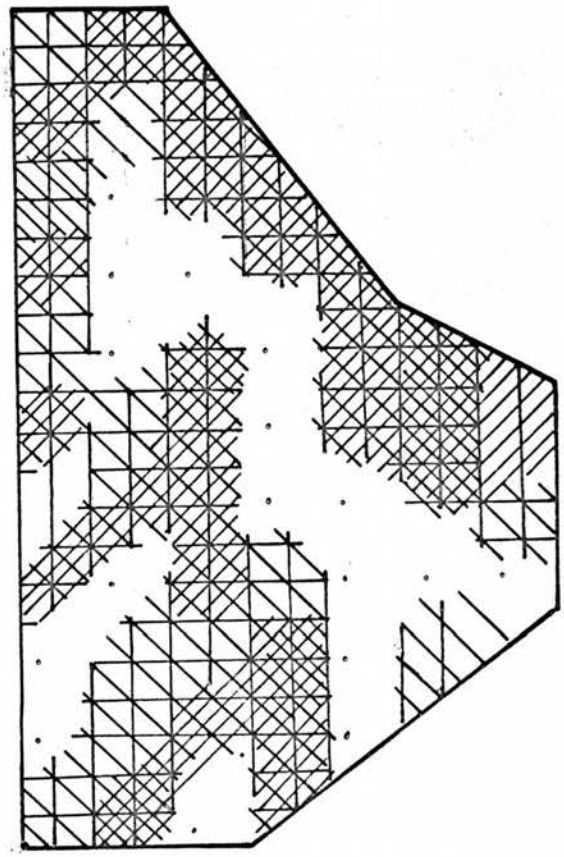
MAP 4,b.

ARCHERFIELD — 14



MAP 4,c.

ARCHERFIELD—14



Field: Archerfield 14.

Population grid intersection number	Number of cysts recovered in the parent population	Total number of cysts produced on Craigs S1 generation	Defiance S2 generation	H1 ex adg	Fa ex spg	H2 ex mlt	H2 ex sct	H1H2 adg x mlt	H1H2 adg x sct
1	2	3	4	5	6	7	8	9	10
1	144	14	125	0	0	110	50	0	
2	67	0							
3	3	0							
4	6	22	56	1	3	38	18	0	0
5	5	3	60	0		55			
6	1	0		1	2	56	42	0	0
7	3	7	10	1	0	66	29	0	0
8	26	18	58	0	4	88	54	0	0
9	30	9	29	2	1	42	31	0	0
10	165	116	28	0	4	58	42	0	0
11	226	51	30	1	1	56	76	0	0
12	206	39	80	1	6	88	28	0	
13	83	59	70						
14	389	0							
15	5	1	0						
16	8	0							
17	120	45	37	1	1	48	24	0	0
18	139	15	34	1	2	13	34	0	0
19									
20	287	21	35	0	1	66	49	0	0
21	110	24	52	0	1	99	15	0	0
22	145	47	147	2	2	53	23	0	0
23	5	0							
24	13	105	49	1	2	0	60	0	0
25	13	50	80	1	0	59	67	0	0
26	28	11	54	0	5	119	46	0	0
27	4	31	17	0	4	74	13	0	0
28	15	26	40	0	2	36	41	0	0
29	49	216	25	2	2	58	40	0	0
30	2	0							
31	2	90	27	0	2	19	74	0	0
32	65	47	77	0	2	45	63	0	0
33	56	115	37	1	6	70	31	0	0
34	9	5	42	0	13	60	61		

Field: Archerfield 14 (Contd.)

1	2	3	4	5	6	7	8	9	10
35	55	0							
36	0								
37	4	0							
38	8	9	39	0	0	25	30	0	0
39	86	45	26	2	3	24	23	0	0
40	9	12	16	1	3	48	71	0	0
41	4	0							
42	0								
43	0								
44	2	0							
45	8	66	42	1	3	62	31	0	0
46	13	44	55	1	2	26	33	0	0
47	2	33	51	2	4	21	23	0	0
48	4	37	37	12	2	54	23	0	0
49	1	39	73	4	4	40	74	0	0
50	0								
51	10	56	52	0		54		0	0
52	15	0							
53	9	62	116	1	7	115	43	0	0
54	1	61		0		1			
Means	0·127	48·16	46·51	0·68	2·84	51·53	44·15	-	-
Maximum	0·972	216	147	12	13	119	74	-	-
Minimum	0·00	0	0	0	0	0	15	-	-

Map 5a.

Field: Archerfield 15. O.S. Number,[1] 1200.

Location: Archerfield, Dirleton, East Lothian.

Area: 20·25 acres.

Soil type and drainage:[2] Raised beach sands and gravel, freely drained.

Height above sea level: 150 feet approximately.

Cropping history:
1960-61 Barley.
1961-62 Fallow.
1962-63 Early Potatoes.
1963-64 Early Potatoes.
1964-65 Wheat.

Date of soil sampling: December, 1964.

Spacing between sampling points: 30 x 30 yards.

Total number of soil samples collected: 70.

Average cyst density for the field: 0·326 cysts per gm. air-dried soil.

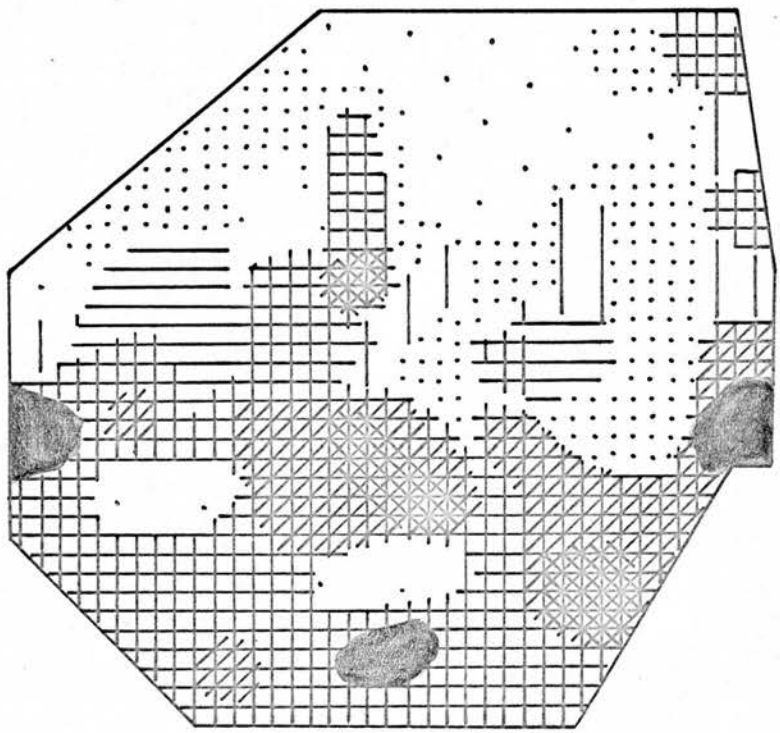
1. Ordnance survey map 1:25000, sheet No. NT 5084, Revised edit. 1965.

2. Soil survey of Scotland, 1966.

Observations: There seem to be several foci of comparable age but not associated with any broad zones of continuous spread. There are also several younger foci in the lightly infested area. There appears some scope for further spread and increase in the infestation, particularly towards the northern region of the field.

MAP 5,a.

ARCHERFIELD—15



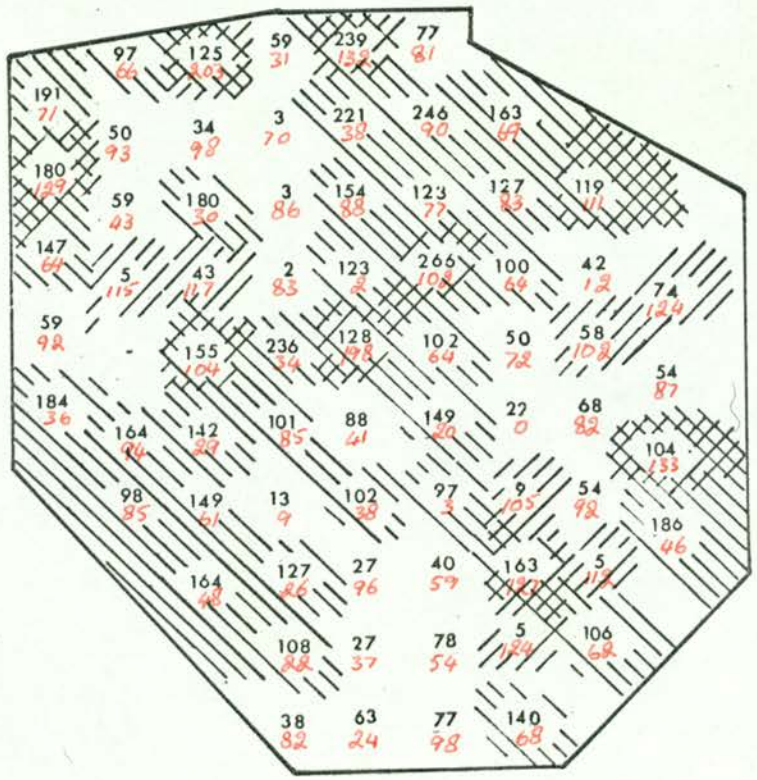
Cysts per gram of soil

- 0·91-1·120
- -0·900
- -0·700
- -0·500
- -0·350
- -0·240
- -0·150
- 0·00-0·080

90 Yards

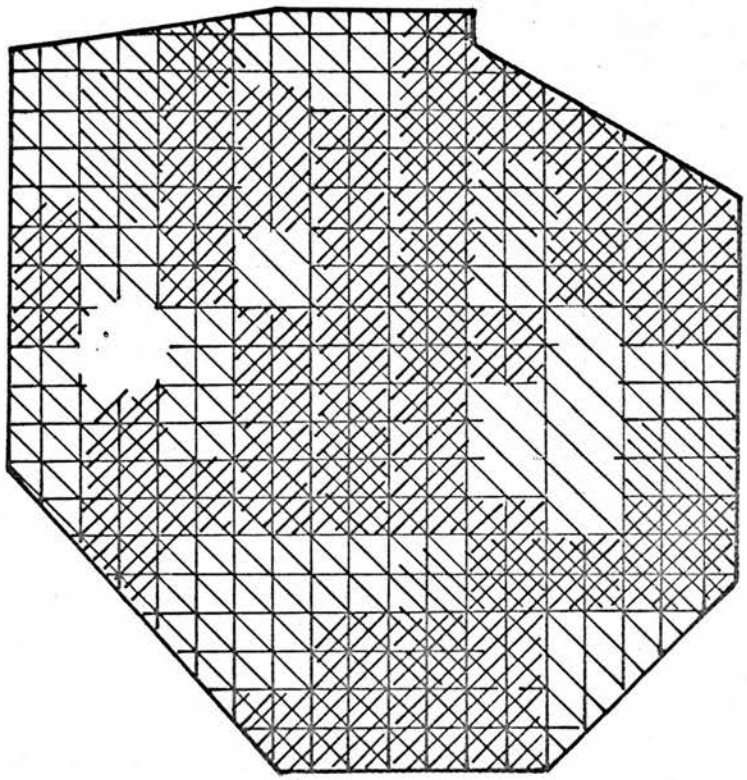
MAP 5,b.

ARCHERFIELD—15



MAP 5,c.

ARCHERFIELD—15



Field: Archerfield 15

Population grid intersection number	Number of cysts recovered in the parent population	Total number of cysts produced on Craigs S1 generation	Defiance S2 generation	H1 ex adg	Fa ex spg	H2 ex mlt	H2 ex sct	H1H2 adg x mlt	H1H2 adg x sct
1	2	3	4	5	6	7	8	9	10
1	6	184	36	1	1	57	39	0	-
2	9	59	92	0	2	39	50	0	-
3	16	147	64	1	2	65	65	0	-
4	29	180	129	0	0	48	48	-	-
5	179	191	71	1	10	115	113	0	-
6	36	97	66	0	0	57	67	-	-
7	11	53	93	2	1	107	82	0	-
8	15	89	43	3	1	108	71	0	-
9	17	5	115	1		12	38	0	-
10	13	0							
11	102	164	94	0	2	57	65	0	-
12	25	98	85	0	2	29	34	0	-
13	26	169	48	0	0	57	56	0	-
14	13	149	61	1	2	63	19	0	-
15	105	42	29	1	0	42	34	0	-
16	4	155	104	0	1	5	11	0	-
17	7	43	117	0	2	68	82	0	-
18	42	180	30	1	2	45	50	0	-
19	17	34	98	0	2	32	41	0	0
20	54	125	203	3	2	23	87	0	0
21	47	59	31	0	0	54	75	0	0
22	20	3	70	1	4	118	46	0	0
23	42	3	86	0	3	20		0	
24	30	2	83	0		11			
25	41	236	34	1	3	9	30	0	0
26	149	101	85	0	7	36	69	0	0
27	74	133	9	1	5	97	137	0	0
28	51	127	26	1	1	22	26	0	0
29	53	108	22	0	1	19	133	0	-
30	9	38	82	0	11	73	80	0	-
31	46	63	24	0	3	30	35	0	0
32	80	27	37	0	3	78	114	0	-
33	64	27	96	0	-	108	52	0	0
34	95	102	38	2	1	63	71	0	0
35	41	88	41	2	4	77	110	0	0
36	22	128	198	0	5	52	15	0	0
37	71	123	37	0	2	13	26	0	0
38	49	154	88	0	3	69	55	0	0
39	25	221	38	0	2	91	12	0	0
40	44	239	132	0	1	66	52	0	0

Field: Archerfield 15 (Contd.)

1	2	3	4	5	6	7	8	9	10
41	225	77	81	0	2	42	81	0	0
42	38	246	90	2	7	101	41	0	0
43	35	123	77	1	3	58	38	0	-
44	138	266	102	2	2	14	89	0	-
45	54	112	64	2	2	79	85	0	-
46	150	149	20	1	3	65	60	0	-
47	139	97	3	0	4	52	68	0	-
48	104	40	59	2	0	28	41	0	-
49	109	78	54	2	2	58	93	0	-
50	96	77	98	0	4	43	116	0	-
51	182	140	68	1	4	34	91	0	-
52	8	5	124		2	24			
53	6	163	127	2	2	35	57	0	-
54	163	9	105	1	3	19	81	0	-
55	130	22	0	0	1	22			
56	151	50	72	0	2	5	85	-	-
57	50	100	64	1	0	30	132	0	-
58	112	127	83	3	1	65	93	0	-
59	113	163	69	1	4	44	49	0	-
60	147	119	111	1	2	81	70	0	-
61	105	42	12	2	4	42	40	0	-
62	1	58	102	0		13			
63	4	2	82	0		27			
64	59	68	92	1	1	41	111	0	-
65	65	54	112	2	4	17	64	0	0
66	91	5	62	0		8			
67	134	126	46	3	3	123	58	0	-
68	70	104	133	2	1	131	83	0	-
69	189	54	87	1	7	150	85	0	-
70	95	74	124	0	1	38	64	-	-
Means	0·326	101·0	72·7	0·48	2·41	51·14	66·17	-	-
Max.	1·125	266	203	3	11	150	137	-	-
Min.	0·00	0	2	0	0	5	8	-	-

Map 6a.

Field: Ferrygate, O.S. Number,[1] 2967.

Location: Ferrygate, North Berwick, East Lothian.

Area: 33·58 acres.

Soil type and drainage:[2] Raised beach sand and gravel, freely drained.

Height above sea level: 100 feet approximately.

Cropping history:
1960-61 Ryegrass.
1961-62 Sugarbeet.
1962-63 Wheat.
1963-64 Early Potatoes.
1964-65 Barley.

Date of soil sampling: December, 1964.

Spacing between sampling points: 30 x 30 yards.

Total number of soil samples collected: 120.

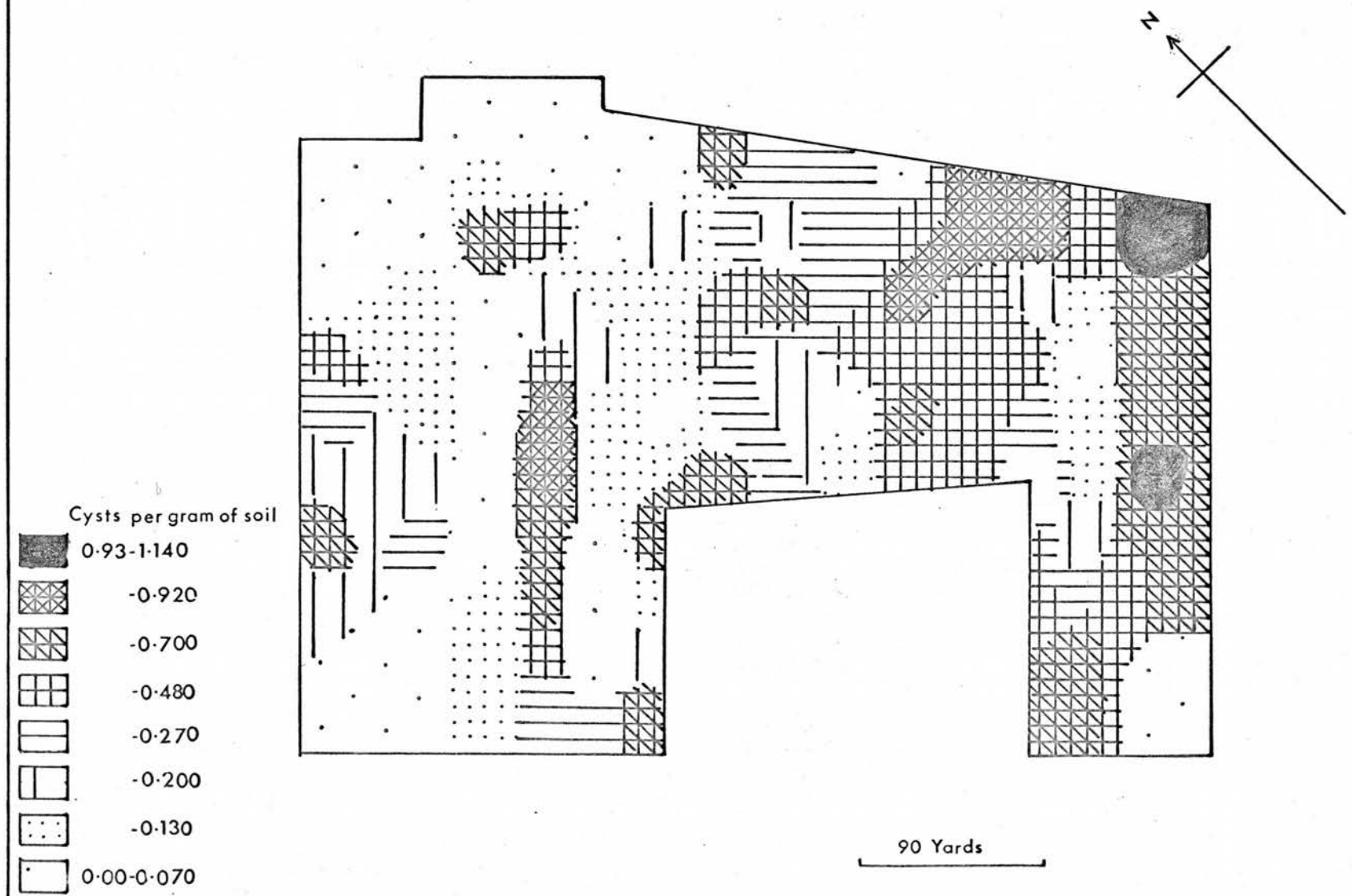
Average cyst density for the field: 0·261 cysts per gm. air-dried soil.

1. Ordnance Survey map 1:25000 sheet No. NT 4284, Revised edit. 1965.

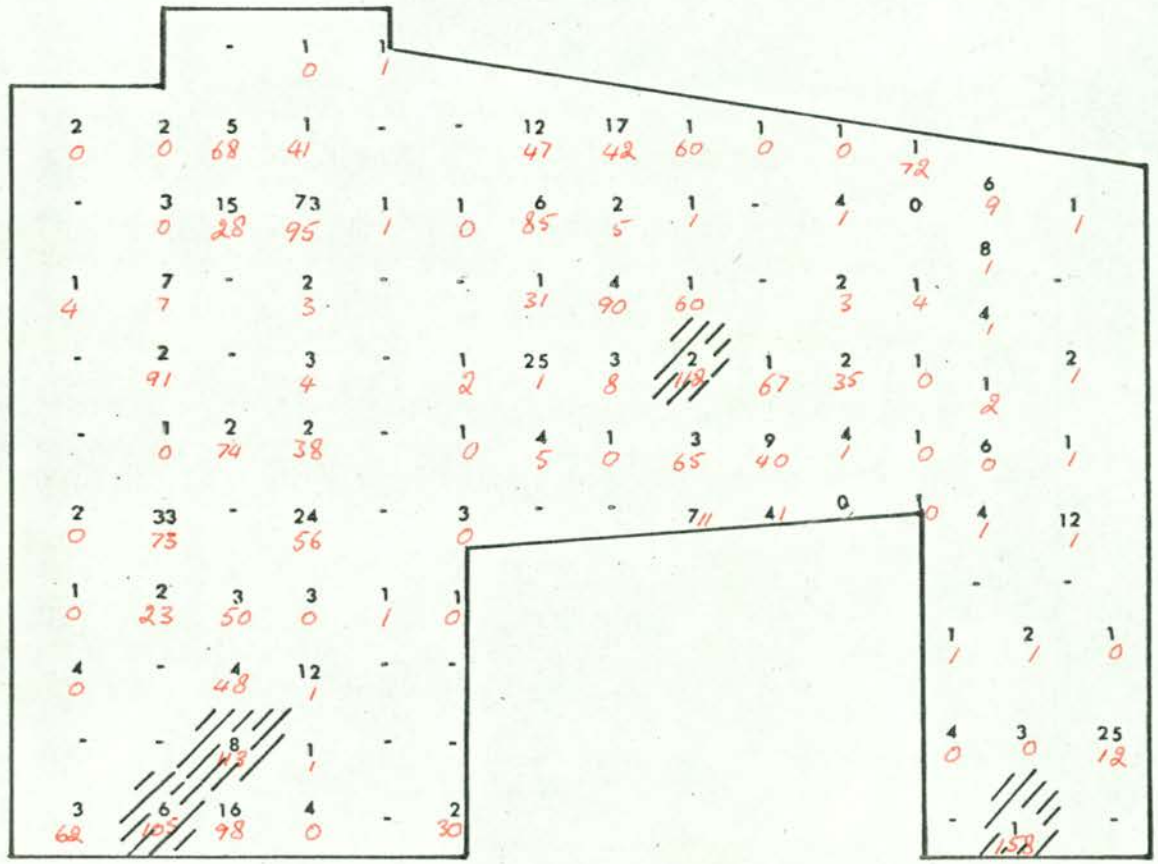
2. Soil survey of Scotland, 1966.

Observations: The principal foci of infestation appeared to lie near the east side of the field. Subsidiary foci are developing over the rest of the field. The zones of continuous spread extend in a north/south direction, the direction in which the field is normally ploughed. There appears to be considerable scope for further spread and increase in the level of cyst density and area of infestation.

FERRYGATE

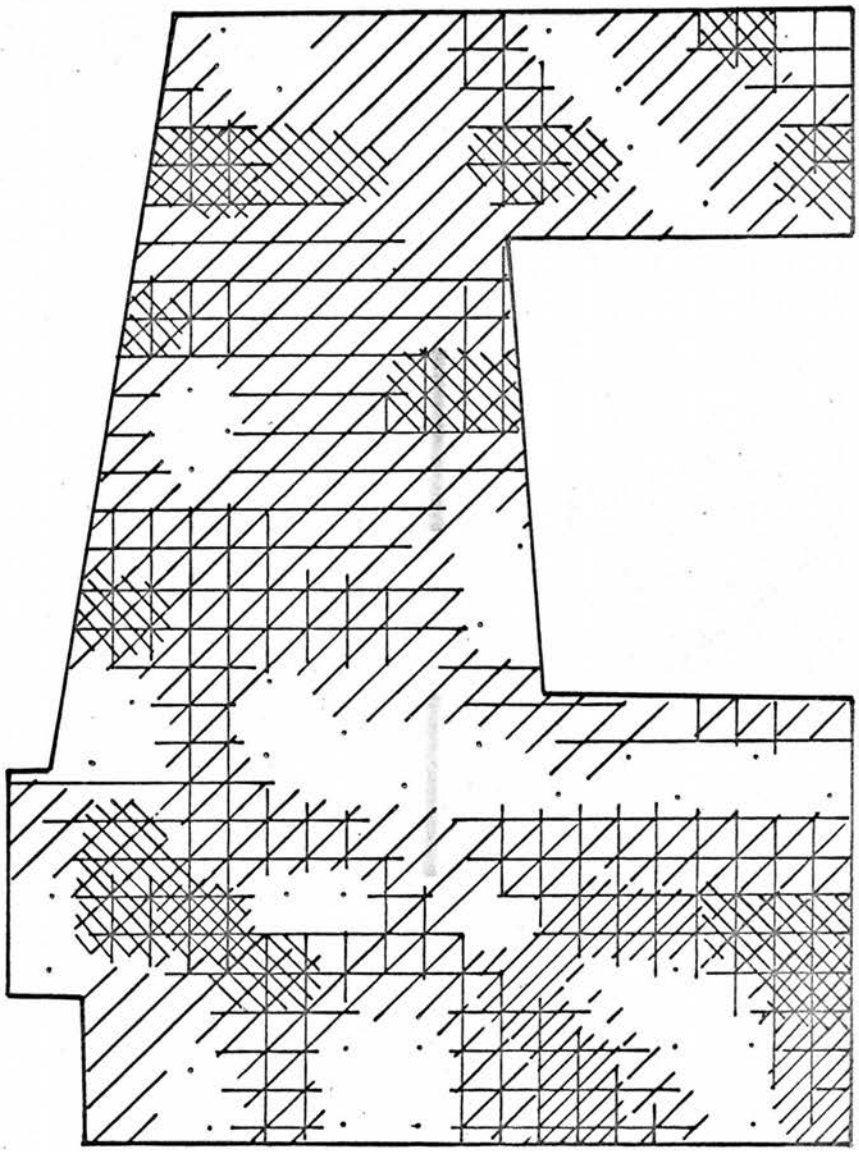

N
Cysts per gram of soil
0·93-1·140
-0·920
-0·700
-0·480
-0·270
-0·200
-0·130
0·00-0·070
90 Yards

FERRYGATE


- 1 1
0 1
2 2 5 1 - - 12 17 1 1 1 1
0 0 68 41 47 42 60 0 0 72
- 3 15 73 1 1 6 2 1 - 4 0 6 1
0 28 95 1 0 85 5 1 1 9 1
8
1 7 - 2 - - 1 4 1 - 2 1 -
4 7 3 31 90 60 3 4
4
- 2 - 3 - 1 25 3 2 1 2 1 2
91 4 2 118 67 35 0 1
2
- 1 2 2 - 1 4 1 3 9 4 1 6 1
0 74 38 0 5 0 65 40 1 0 0 1
2 33 - 24 - 3 - - 71 41 0 10 4 12
0 73 56 0 1
- -
1 2 3 3 1 1
0 23 50 0 1 0
1 2 1
1 1 0
4 - 4 12 - -
0 48 1
- - 8 1 - -
48 1
4 3 25
0 0 12
3 6 16 4 - 2 1
62 105 98 0 30 158 -

MAP 6,c.

FERRYGATE



Field: Ferrygate.

Population grid intersection number	Number of cysts recovered in the parent population	Total number of cysts produced on Craigs Defiance S1 generation	S2 generation	H1 ex adg	Fa ex spg	H2 ex mlt	H2 ex sct	H1H2 adg x mlt	H1H2 adg x sct
1	2	3	4	5	6	7	8	9	10
1	13	3	62	1		33			-
2	4	9	0						
3	39	4	0						
4	163	1	0	1	0	28	0	-	
5	58	2	0	0					
6	63	0							
7	78	0			0	41	10	-	
8	8	1	4	0		28			
9	1	0							
10	4	2	0						
11	10	2	0						
12	7	3	0						
13	21	7	7	0	6	15	49	0	-
14	34	2	91	0		52			
15	30	1	0						
16	39	33	73	2	0	10	45	0	-
17	64	2	23			0	22		
18	11	0							
19	8	0							
20	12	6	105	2	9	66	60	0	
21	24	16	98	0	1	31	38	-	-
22	27	8	113	0	7	63	36	0	-
23	29	4	48	1		42		-	
24	7	3	50	1		13			
25	0								
26	2	2	74	0		3			
27	3	0							
28	5	0							
29	165	15	28	1	11	41	48	-	-
30	31	5	60	0	20	69	7	-	-
31	8	0							
32	2	1	0						
33	15	1	47	0		25			
34	118	73	95	1	19	65	54	-	-
35	58	2	3	0	0	1	23	-	-
36	141	3	4	0		30			
37	225	2	38	0	0	0	18	-	-
38	242	24	56	0	0	42	29	-	-

Field: Ferrygate (Contd.)

1	2	3	4	5	6	7	8	9	10
39	205	3	0	0	0	43	1	-	-
40	147	12	1	0	0	38	59	-	-
41	137	1	1	0	0	21	14	-	-
42	67	4	0	0		0			
43	69	0							
44	14	0							
45	7	0							
46	8	1	1	0					
47	26	0							
48	40	0							
49	35	0							
50	28	0							
51	8	1	1						
52	10	0							
53	11	1	1						
54	6	0							
55	39	1	0						
56	38	0							
57	20	1	2						
58	7	1	0						
59	27	3	0	0		1			
60	208	1	0		0	3	25	-	-
61	118	0							
62	38	0					2		-
63	56	2	30	0		20			
64	151	0							
65	72	4	5	0		20			
66	139	25	1	0	0	4	46	-	-
67	128	1	31	0		12			-
68	74	6	85	0	0	3			
69	184	12	47	0	10	18	42	0	0
70	63	17	42	0	0	31	24	-	-
71	51	2	5	0	0	7	18		
72	171	4	90	0	0	12			
73	53	3	8	0		6			
74	48	1	0						
75	72	0							
76	22	7	11	0	0	36	72		-
77	17	2	65	0		32			
78	80	3	112	0		23	0		
79	61	1	6	0		0			
80	71	1	1						
81	68	1	60	0		40			
82	8	1	0						
83	160	0							
84	240	6	0		0	4	25	-	-
85	136	1	67	0		25			

Field: Ferrygate (Contd.)

1	2	3	4	5	6	7	8	9	10
86	160	9	40	0	2	0	67	-	-
87	138	4	1	0	6	0	51	0	0
88	119	0							
89	92	4	1			27			
90	139	2	35	0		7			
91	79	2	3	0		7			
92	221	4	1	0	0	40	1	-	-
93	220	1	0		3	47	37	0	0
94	249	1	72	0		20	0		
95	194	1	0					-	
96	51	1	4	0		19			
97	80	1	0						
98	61	1	0						
99	70	1	0						
100	141	4	0	0	3				
101	174	1	1	0					
102	76	0							
103	44	4	1	0	2	0	0	-	-
104	27	6	0	0	1	10	2	-	-
105	38	1	2	0					
106	15	4	1	0					
107	27	8	1	0	5	0	0	0	0
108	132	6	9	1	1	3	3	-	-
109	282	1	1	0					
110	147	6	0						
111	199	2	1	0					
112	163	1	1	0					
113	344	12	1	0	0	10	14	-	-
114	183	0							
115	120	2	1	0					
116	5	3	0	0		0			
117	12	1	158	0		9			
118	26	0							
119	17	25	12	0	4	1	1	0	0
120	192	1	0	-					
Means	0·261	3·87	23·0	0·24	4·26	18·95	26·19	-	-
Max.	1·146	73	158	2	20	69	72	-	-
Min.	0·00	0	0	0	0	0	0	-	-

Map 7a.

Field: Kettle, O.S. Number,[1] 0021.

Location: Annfield Mains, Kettle, Fife.

Area: 8·07 acres.

Soil type and drainage:[2] Basalt, imperfectly drained.

Height above sea level: 400 feet approximately.

Cropping history:
1960-61 Grass.
1961-62 Sugarbeet.
1962-63 Oats.
1963-64 Maincrop Potatoes.
1964-65 Sugarbeet.

Date of soil sampling: July, 1965.

Spacing between sampling points: 30 x 30 yards.

Total number of soil samples collected: 45.

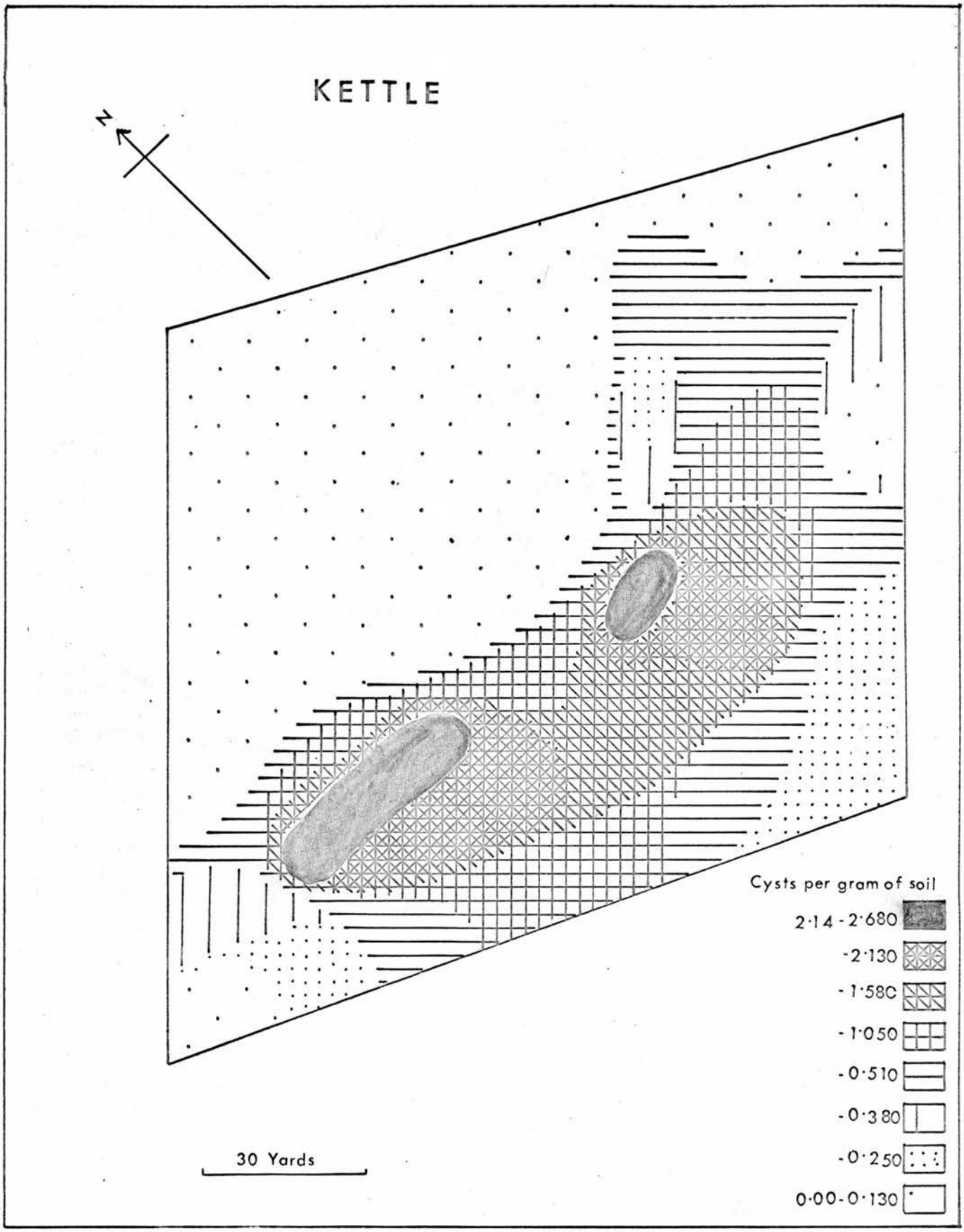
Average cyst density for the field: 0·506 cysts per gm. air-dried soil.

1. Ordnance Survey map 1:25000 Sheet No. NT 3107, revised edit. 1965.

2. Geological Survey of Scotland, Sheet No.40, 1950 edit.

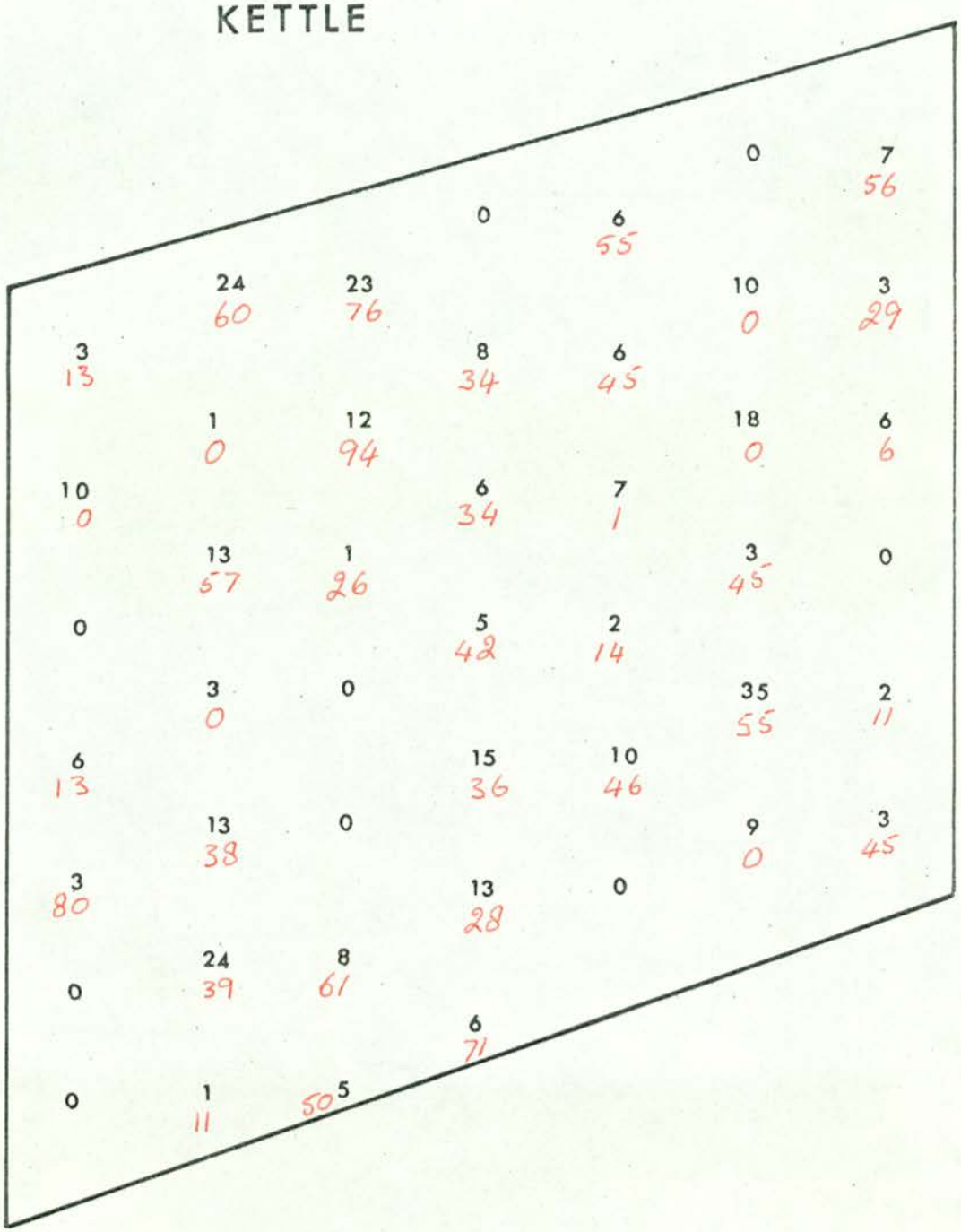
Observations: There appear two foci almost forming one principal focus of infestation, which is surrounded by a broad zone of continuous spread. This infestation has spread more towards the south and north-eastern corner of the field. Otherwise, there is considerable scope for further spread and increase of infestation. There is a notable absence of secondary foci in the north-western quarter of the field, where, it appears that for no apparent reason further spread is restricted.

MAP 7,a.


KETTLE
N
Cysts per gram of soil
2·14 - 2·680
-2·130
- 1·580
- 1·050
- 0·510
- 0·380
- 0·250
0·00 - 0·130
30 Yards

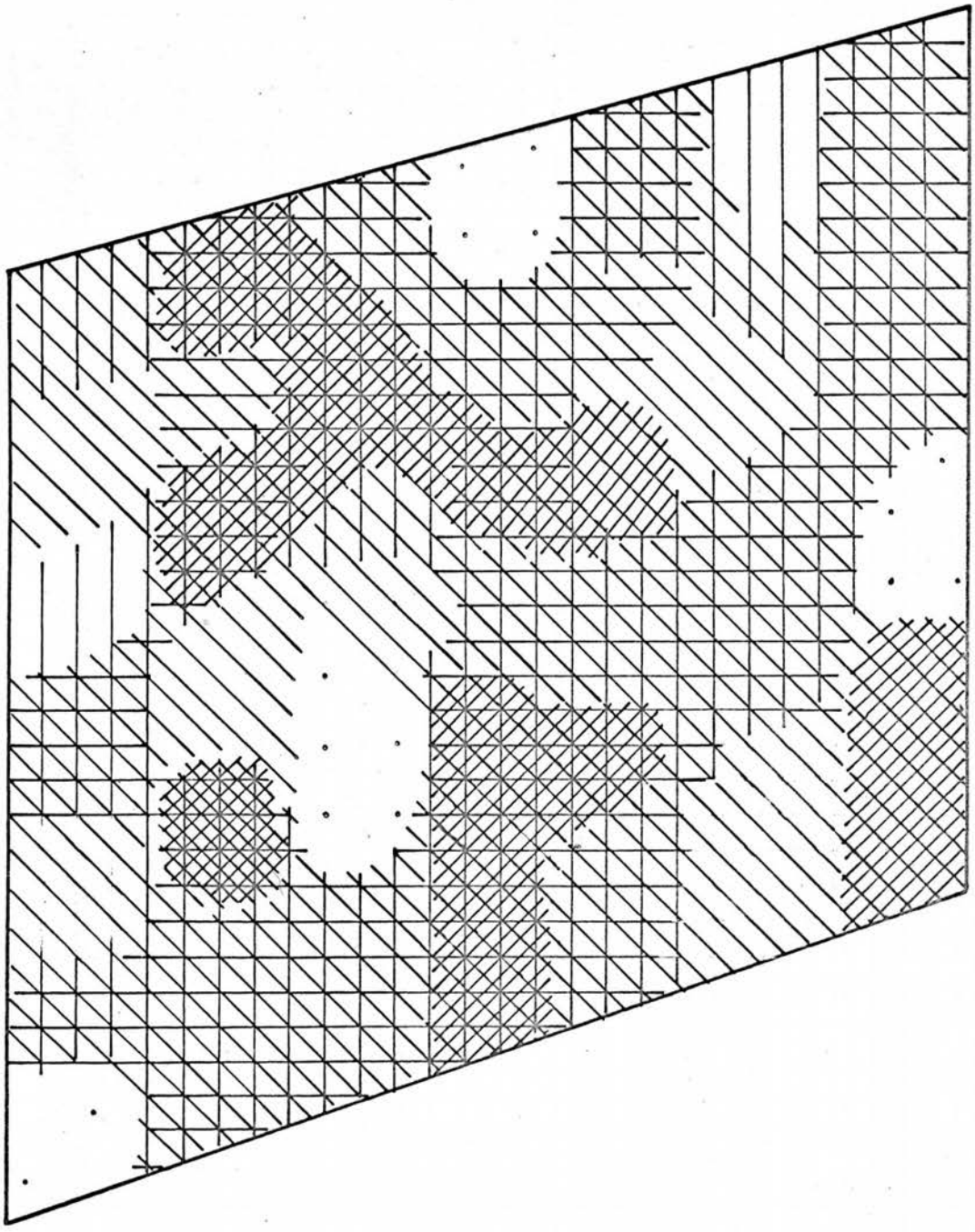
MAP 7,b.

KETTLE



MAP 7,c.

KETTLE



Field: Kettle

Population grid intersection number	Number of cysts recovered in the parent population	Total number of cysts produced on Craigs Defiance S1 generation	S2 generation	H1 ex adg	Fa ex spg	H2 ex mlt	H2 ex sct	H1H2 adg x mlt	H1H2 adg x sct
1	2	3	4	5	6	7	8	9	10
1	6	3	13	0		8			
2	1	10	0						
3	6	58	0	0	0	27			
4	5	6	13	0	0	5	75	-	-
5	33	3	80	0	0	23			
6	82	24	0	0	0	11	55	-	-
7	5	0							
8	59	1	11	0	0	29	41	-	-
9	717	24	39	0	0	40	19	-	-
10	263	13	38	2	1	19	29	0	0
11	7	3	0						
12	3	13	57	0	2	32	25	0	0
13	6	1	0	0		0	0	-	-
14	4	24	60	0	3	5	57	0	0
15	18	23	76	0	0	2	3	-	-
16	5	12	94	0	3	23	58	0	0
17	6	1	26	0		18			
18	19	3	0						
19	805	3	0	0	0	0	1	-	-
20	537	8	61	0	0	23	9	-	-
21	121	5	50	0	0	10	19	-	-
22	168	6	71	0	4	6	28	0	0
23	599	13	28	0	12	35	29	0	0
24	162	15	36	0	2	45	16	0	0
25	32	5	42	0	0	35	53	-	-

Field: Kettle (Contd.)

1	2	3	4	5	6	7	8	9	10
26	7	6	34	0	2	1	44	0	0
27	2	8	34	0	0	2	40	-	-
28	11	0							
29	139	6	55	0	0	25	36	-	-
30	64	6	45	0	0	0	39	-	-
31	61	7	1	1	1	0	0	-	-
32	707	2	14	0	0	19	46	-	-
33	340	10	46	0	1	1	13	-	-
34	147	9	0	0	0	0	1	-	-
35	636	35	55	0	0	3	4	-	-
36	327	3	45	0	0	23	11	-	-
37	173	18	0	0	0		0	-	-
38	116	10	0	0	0	2	0	-	-
39	20	0		0		9			
40	14	7	56	0	0	22	18	-	-
41	95	3	29	0	0	16	11	-	-
42	37	6	6	0	0	1	1	-	-
43	134	0							
44	65	2	11	0	35				
45	41	3	45	0	38				
Means	0·506	7·3	33·1	0·29	2·00	16·34	25·48	-	-
Max.	2·683	35	94	2	12	45	75	-	-
Min.	0·003	0	0	0	0	0	0	-	-

Map 8a.

Field: Pitlethie, O.S. Number,[1] 2442.

Location: Pitlethie, Leuchars, Fife.

Area : 17·09 acres.

Soil type and drainage:[2] Old red sandstone, freely drained.

Height above sea level: 100 feet approximately.

Cropping history:

1960-61	Grass.
1961-62	"
1962-63	"
1963-64	Maincrop Potatoes.
1964-65	Turnips.

Date of soil sampling: July, 1965.

Spacing between sampling points: 30 x 30 yards.

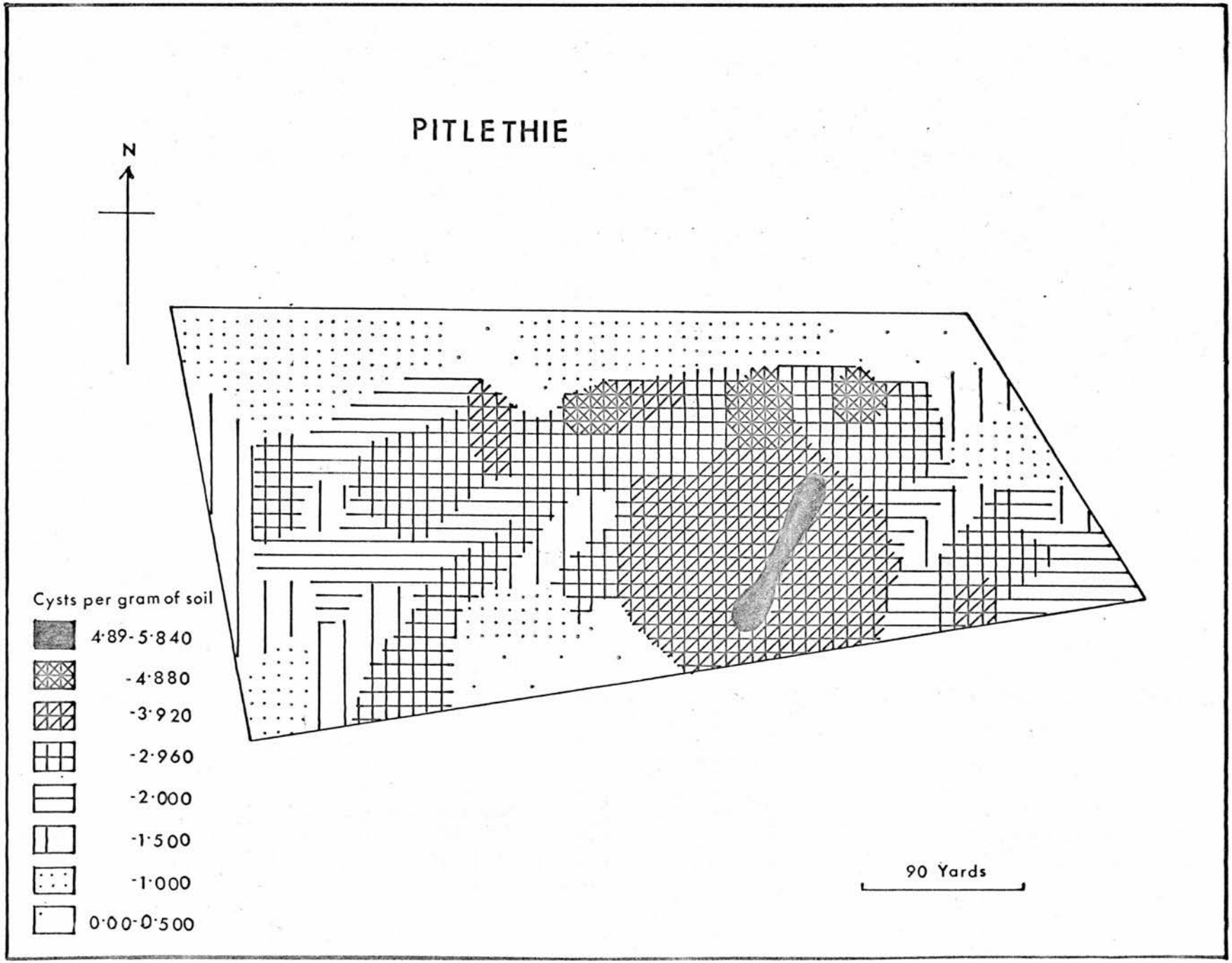
Total number of soil samples collected: 97.

Average cyst density for the field: 2·037 cysts per gm. air-dried soil.

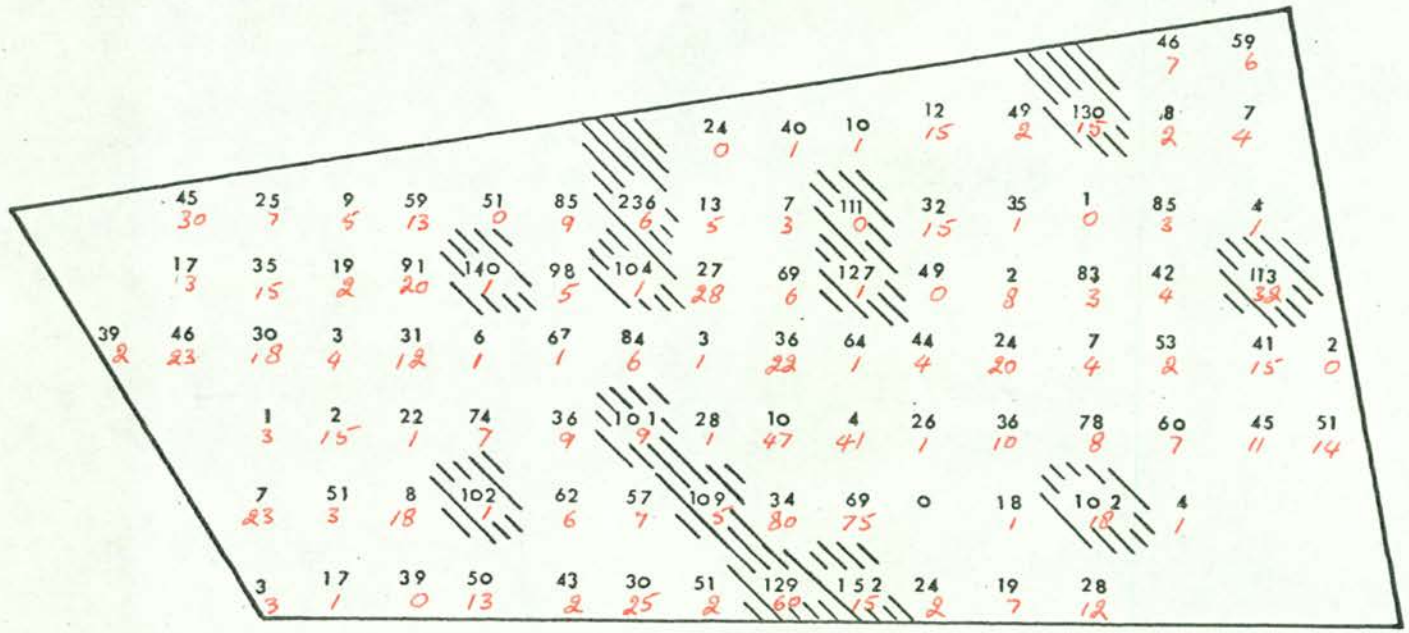
1. Ordnance Survey map, 1:25000, sheet No. NT 4621, Revised edit. 1965.

2. Geological Survey of Scotland, sheet No.49, 1950 edit.

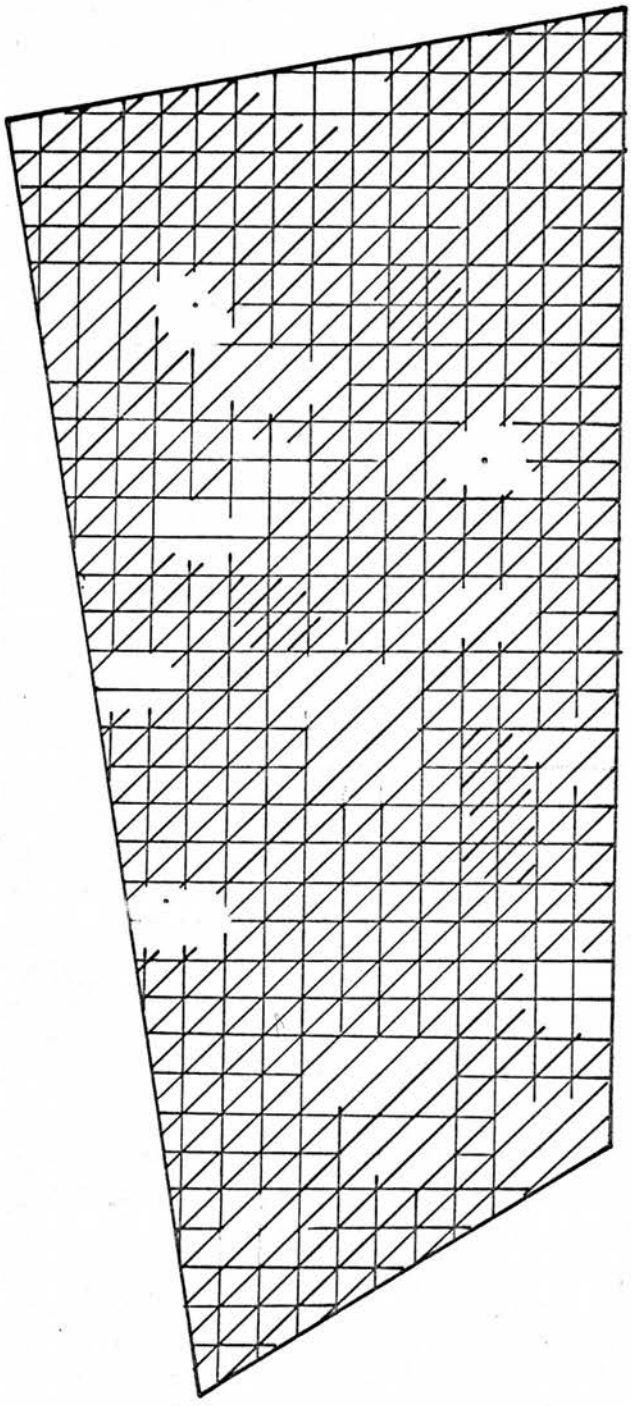
Observations: There is one principal focus of infestation and three secondary foci are in evidence along the north side of the field. The primary focus is surrounded by a broad zone of continuous spread while tertiary and other foci are distributed over much of the remaining area. Although the average level of infestation is fairly high there still appears to be considerable scope for further increase and spread of infestation.


PITLETHIE
N
Cysts per gram of soil
4·89-5·840
-4·880
-3·920
-2·960
-2·000
-1·500
-1·000
0·00-0·500
90 Yards

PITLETHIE


46 7
59 6
24 0
40 1
10 1
12 15
49 2
130 15
8 2
7 4
45 30
25 7
9 5
59 13
51 0
85 9
236 6
13 5
7 3
111 0
32 15
35 1
1 0
85 3
4 1
17 3
35 15
19 2
91 20
140 1
98 5
104 1
27 28
69 6
127 1
49 0
2 8
83 3
42 4
113 32
39 2
46 23
30 18
3 4
31 12
6 1
67 1
84 6
3 1
36 22
64 1
44 4
24 20
7 4
53 2
41 15
2 0
1 3
2 15
22 1
74 7
36 9
101 9
28 1
10 47
4 41
26 1
36 10
78 8
60 7
45 11
51 14
7 23
51 3
8 18
102 1
62 6
57 7
109 5
34 80
69 75
0
18 1
102 12
4 1
3 3
17 1
39 0
50 13
43 2
30 25
51 2
129 60
152 15
24 2
19 7
28 12

MAP 8,c.



PITLETHIE

Field: Pitlethie

Population grid intersection number	Number of cysts recovered in the parent population	Total number of cysts produced on Craigs Defiance S1 generation	S2 generation	H1 ex adg	Fa ex spg	H2 ex mlt	H2 ex sct	H1H2 adg x mlt	H1H2 adg x sct
1	2	3	4	5	6	7	8	9	10
1	14	3	3	0		12			
2	510	7	23	0	0	3	3	-	-
3	398	1	3	0		0			
4	517	30	18	0	0	10	17	-	-
5	864	35	15	0	0	3	2	-	-
6	1178	25	7	0	0	2	18	-	-
7	670	45	30	0	0	5	5	-	-
8	810	17	3	0	0	0	23	-	-
9	748	46	23	0	0	10	1	-	-
10	401	39	2	0	0	5	3	-	-
11	602	9	5	0	0	1	1	-	-
12	580	19	2	0	0	1	4	-	-
13	761	3	4	0		3			
14	456	2	15	0		25			
15	696	51	3	0	0	1	11	-	-
16	108	17	1	0	0	1	19	-	-
17	95	39	0	0	0	2	20	-	-
18	1290	8	18	0	0	7	1	-	-
19	906	22	1	0	0	11	11	-	-
20	1002	31	12	0	0	5	8	-	-
21	1146	91	20	0	0	3	28	-	-
22	966	59	13	0	0	11	3	-	-
23	888	51	0						
24	732	140	1	0	0	9	18	-	-
25	1490	6	1	0	0	7	4	-	
26	1086	74	7	0	0	2	11	-	-
27	690	102	1	0	0	35	3	-	-
28	285	50	13	0	0	5	6	-	-
29	270	43	2	0	0	8	13	-	-
30	1180	62	6	1	0	7	4	-	-
31	985	36	9	0	0	4	4	-	-
32	1140	67	1	0	0	5	18	-	-
33	1156	98	5	0	0	1	12	-	-
34	1752	85	9	0	0	6	2	-	-
35	1056	236	6	0	0	21	2	-	-

Field: Pitlethie (Contd.)

1	2	3	4	5	6	7	8	9	10
36	972	104	1	0	0	1	1	-	-
37	1092	64	6	0	0	3	0	-	-
38	1010	101	9	0	0	0	5	-	-
39	872	57	7	1	0	2	7	0	0
40	262	30	25	0	0	17	0	-	-
41	174	51	2	0	0	1	13	-	-
42	996	109	5	0	0	5	11	-	-
43	804	28	1	0	0	3	10	-	-
44	990	3	1	0	0	2			
45	1098	27	28	0	0	11	10	-	-
46	1002	13	5	0	0	1	9	-	-
47	45	24	0	0	0	1	0	-	-
48	150	40	1	0	0	2	32	-	-
49	288	7	3	0	0	11	5	-	-
50	310	69	6	1	0	22	4	0	0
51	216	36	22	0	0	13	3	-	-
52	610	10	47	0	0	14	2	-	-
53	608	34	80	0	0	53	0	-	-
54	198	129	60	0	0	5	7	-	-
55	300	152	15	0	0	4	5	-	-
56	66	69	75	0	0	10	24	-	-
57	414	4	41	0		17	1	-	-
58	810	64	1	0	0	8	2	-	-
59	150	127	1	0	0	8	1	-	-
60	96	111	0	0	0	3	0	-	-
61	41	10	1	0	0	5	2	-	-
62	66	12	15	0	0	29	26	-	-
63	120	32	15	0	0	4	3	-	-
64	696	49	0	0	0	23	4	-	-
65	476	44	4	0	0	8	7	-	-
66	792	26	1	0	0	0	1	-	-
67	912	0							
68	98	24	2	0	0	8	4	-	-
69	162	19	7	0	0	3	9	-	-
70	480	18	1	0	0	2	2	-	-
71	684	36	10	0	0	4	3	-	-
72	810	24	20	0	0	2	2	-	-
73	564	2	8	0		8			
74	750	35	1	0	0	2	6	-	-
75	726	49	2	0	0	0	1	-	-

Field: Pitlethie (Contd.)

1	2	3	4	5	6	7	8	9	10
76	726	130	15	0	0	0	22	-	-
77	432	1	0						
78	474	83	3	0	0	2	13	-	-
79	839	7	4	0	0	5	14	-	-
80	786	78	8	2	0	23	6	0	0
81	474	102	18	0	0	5	4	-	-
82	186	28	12	0	0	4	6	-	-
83	210	4	1	0	0	0	3	-	-
84	528	60	7	0	0	6	4	-	-
85	432	53	2	0	0	12	8	-	-
86	600	42	4	0	0	45	3	-	-
87	516	85	3	0	0	19	4	-	-
88	438	18	2	0	0	8	7	-	-
89	438	46	7	0	0	2	12	-	-
90	282	59	6	0	0	12	35	-	-
91	204	7	4	0	0	5	7	-	-
92	438	4	1	0	0	1	17		
93	434	113	32	0	0	17	15	-	-
94	606	41	15	0	0	16	35	-	-
95	648	45	11	0	0	3	9	-	-
96	300	51	14	0	0	7	5	-	-
97	312	2	0	0	0	1	1		
Means	2·037	46·91	10·31	73	-	6·95	7·84	-	-
Max.	5·840	236	80	1	-	53	35	-	-
Min.	0·035	1	0	0	-	0	0	-	-

Map 9a.

Field : Woodbank, O.S. Number,[1] 8039A.

Location: Woodbank, Markinch, Fife.

Area : 12·19 acres.

Soil type and drainage:[2] Basalt, imperfectly drained.

Height above sea level: 300 feet approximately.

Cropping history:
1960-61 Grass.
1961-62 Mangolds and Beetroots.
1962-63 Barley.
1963-64 Maincrop Potatoes.
1964-65 Beetroot.

Date of soil sampling: November, 1965.

Spacing between sampling points: 30 x 30 yards.

Total number of soil samples collected: 69.

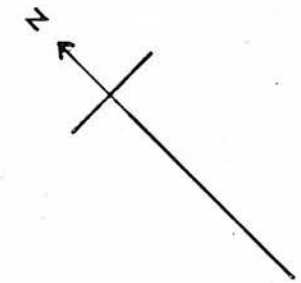
Average cyst density for the field: 0·120 cyst per gm. air-dried soil.

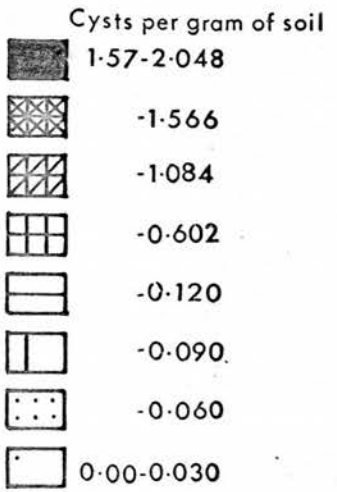
1. Ordnance Survey map, 1:25000 sheet No. NT 3399, Revised edit. 1965.

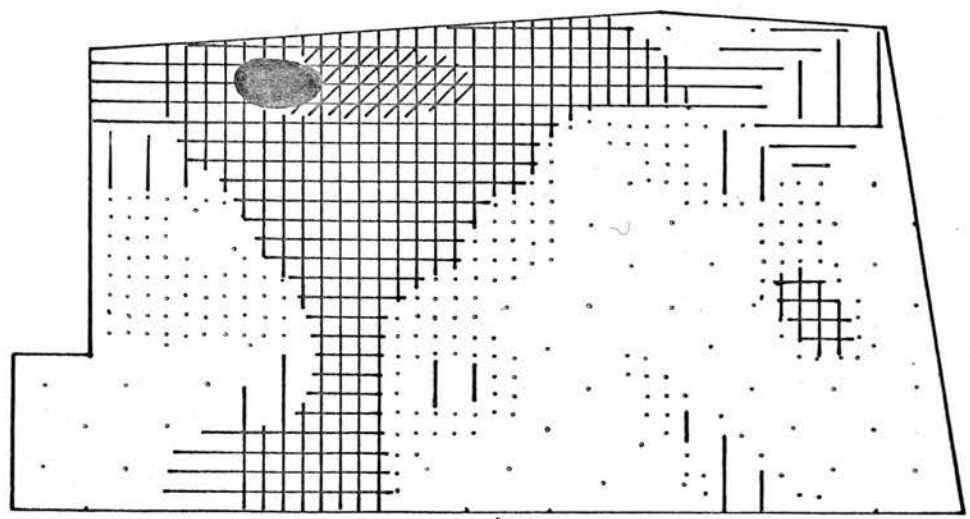
2. Geological Survey of Scotland, sheet No.40, 1950 edit.

Observations: The principal focus of infestation lies near the eastern side of the field, surrounded by a zone of continuous spread. This is extended more or less in a north/south direction, along which axis the field is normally cultivated. Secondary and tertiary foci are developing in lightly infested parts of the field. Cyst density in the most heavily infested area is still quite low as compared to some of the other ware potato growing fields in this region. Obviously there is considerable scope for further spread and increase of infestation. The field is exposed to strong winds, particularly from the western side.

WOOD—BANK

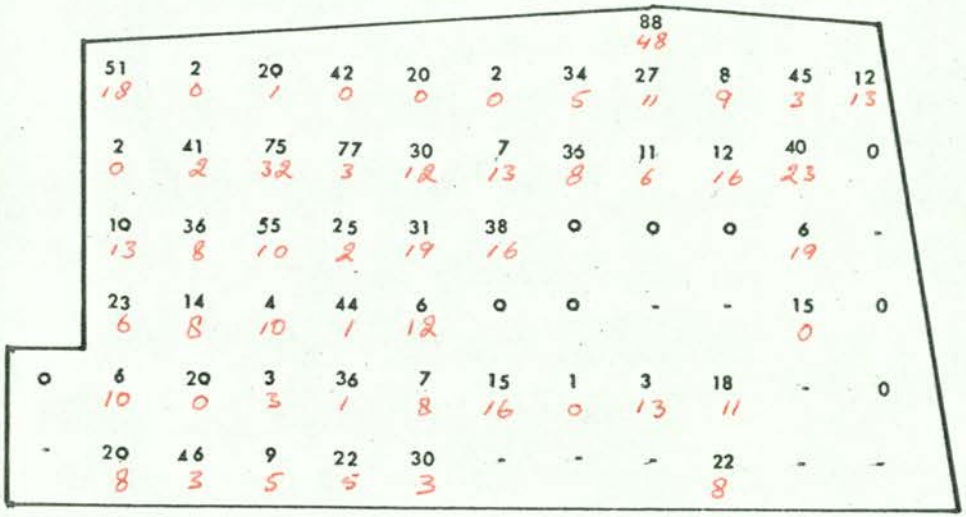






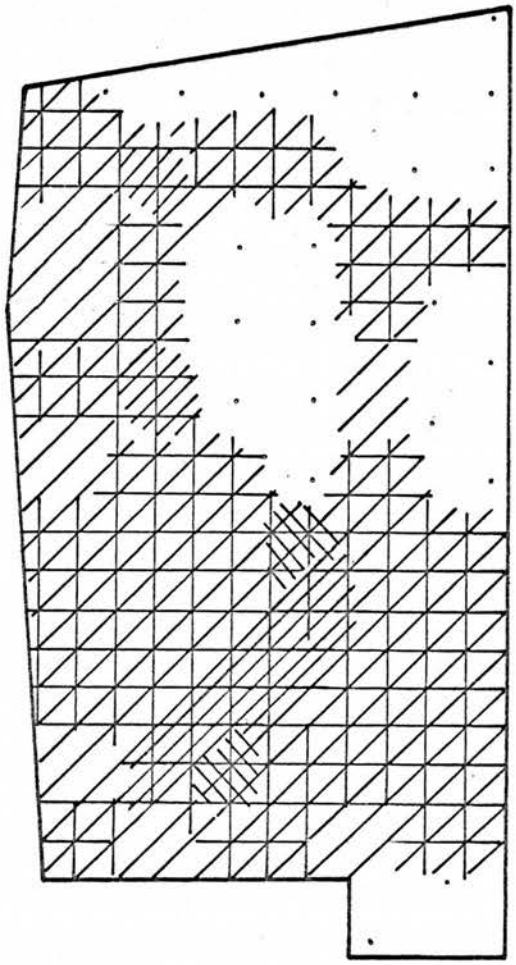
90 Yards

WOOD BANK


88
48
51
18
2
0
20
1
42
0
20
0
2
0
34
5
27
11
8
9
45
3
12
13
2
0
41
2
75
32
77
3
30
12
7
13
36
8
11
6
12
16
40
23
0
10
13
36
8
55
10
25
2
31
19
38
16
0
0
0
6
19
-
23
6
14
8
4
10
44
1
6
12
0
0
-
-
15
0
0
0
6
10
20
0
3
3
36
1
7
8
15
16
1
0
3
13
18
11
-
0
-
20
8
46
3
9
5
22
5
30
3
-
-
-
22
8
-
-

MAP 9, c.

WOOD – BANK



Field: Woodbank

Population grid intersection number	Number of cysts recovered in the parent population	Total number of cysts produced on Craigs Defiance S1 generation	S2 generation	H1 ex adg	Fa ex spg	H2 ex mlt	H2 ex sct	H1H2 adg x mlt	H1H2 adg x sct
1	2	3	4	5	6	7	8	9	10
1	0								
2	0								
3	14	22	8	0	0	6	10	-	-
4	0								
5	0								
6	0								
7	3	30	3	0	0	28	2	-	-
8	55	22	5	0	0	4	9	-	-
9	68	9	5	0	0	6	1		
10	18	46	3	0	0	15	6	-	-
11	4	20	8	0	0	3	2	-	-
12	0								
13	3	0							
14	2	6	10	0	0	6	6		
15	52	20	0	0	0	1	2	-	-
16	14	3	3	0		0		-	
17	56	36	1	0	0	1	4	-	- -
18	13	7	8	0	0	7	2	-	-
19	8	15	6	0	0	0	7	-	-
20	1	1	0						
21	7	13	13	0	0	1	1	-	-
22	3	18	11	0	0	1	17	-	-
23	0								
24	3	0							
25	1	0							
26	27	15	0	0	0	0	6	-	-
27	0								
28	0								
29	3	0							
30	1	0							
31	6	6	12	0	1	3	0	-	
32	79	44	1	2	0	9	1	0	0
33	11	4	10	0	0	1	4	-	
34	9	14	8	0	0	2	3	-	-
35	10	23	6	0	0	2	1	-	-
36	6	10	13	0	0	11	0	-	-
37	1	36	8	0	2	0	15	0	0
38	33	55	10	1	0	8	4	-	-

Field: Woodbank (Contd.)

1	2	3	4	5	6	7	8	9	10
39	57	25	2	0	0	0	12	-	-
40	29	31	19	0	0	4	10	-	-
41	11	38	16	0	0	4	2	-	-
42	6	0							
43	1	0							
44	2	0							
45	9	6	19	0	0	0	0		
46	0								
47	5	0							
48	22	40	23	2	0	7	3	0	0
49	17	12	16	0	0	2	7	-	-
50	9	11	6	0	0	0	9	-	-
51	4	36	8	1	0	1	11	-	-
52	28	7	13	0	0	0	6	-	-
53	52	30	12	0	0	3	1	-	-
54	52	77	3	0	0	3	0	-	-
55	110	65	32	0	0	3	0	-	-
56	26	41	2	1	0	2	2	-	-
57	12	2	0	0					
58	23	51	18	0	0	3	2	-	-
59	78	2	0	0	0				
60	205	20	1	0	0	4	4	-	-
61	166	42	0	0	0	0	9	-	-
62	185	19	0	0	0	1	4	-	-
63	70	2	0	0					
64	64	34	5	0	0	1	2	-	-
65	4	94	48	0	0	20	6	-	-
66	55	26	11	0	0	4	14	-	-
67	20	8	9	0	0	0	10		
68	17	45	3	0	0	0	2	-	-
69	16	12	13	0	0	0	1	-	-
Means	0·120	23·0	10·26	0·12	-	3·88	4·75	-	-
Max.	2·050	65	48	2	1	28	17	-	-
Min.	0·00	0	0	0	0	0	0	-	-

Map 10a.

Field: Blackhall, O.S. Number,[1] 0003.

Location: Blackhall, Dunfermline, Fife.

Area: 19·27 acres.

Soil type and drainage:[2] Basalt, imperfectly drained.

Height above sea level: 300 feet approximately.

Cropping history:

1960-61	Grass.
1961-62	Oats.
1962-63	Maincrop Potatoes.
1963-64	Wheat.
1964-65	Grass.

Date of soil sampling: November, 1965.

Spacing between sampling points: 30 x 30 yards.

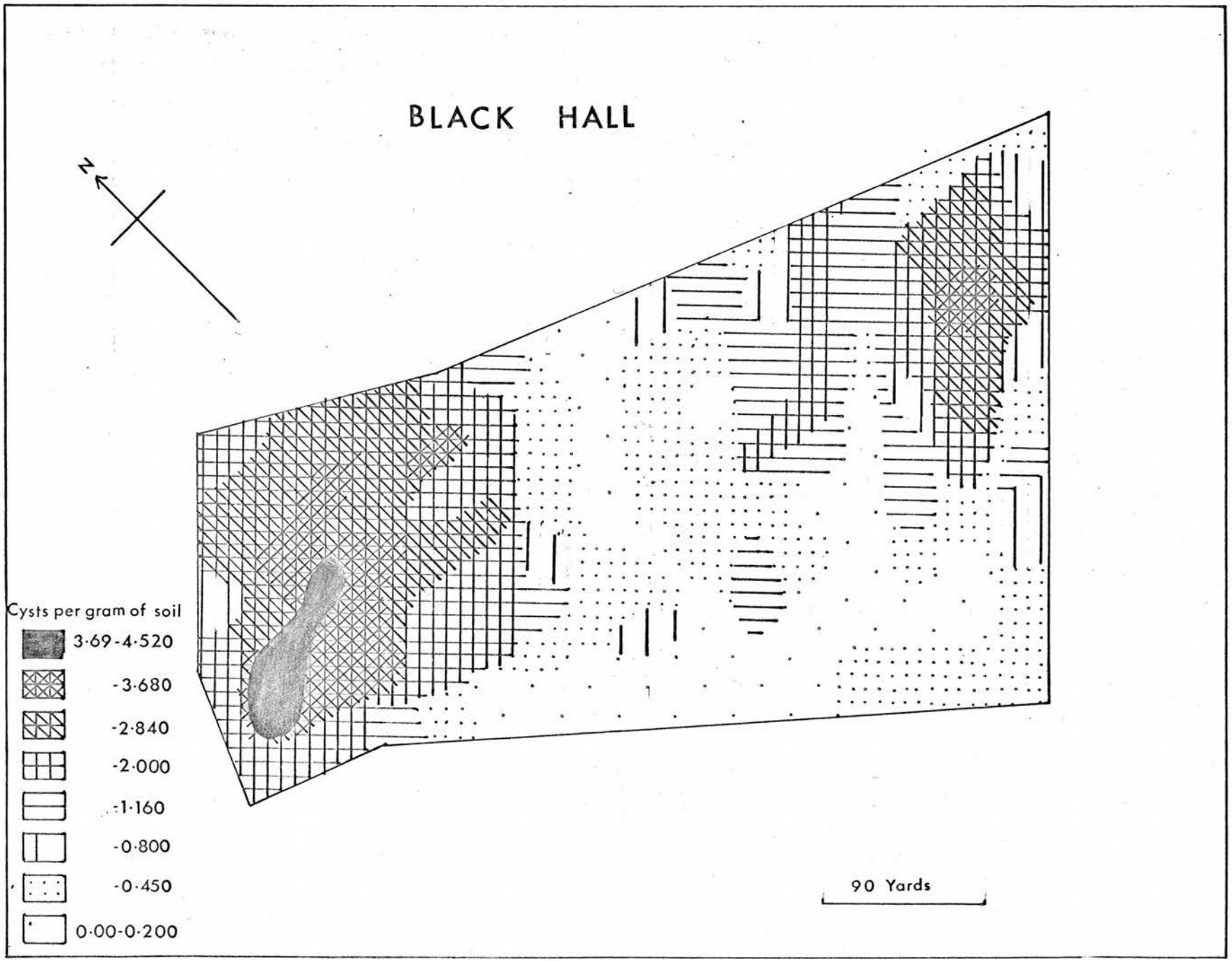
Total number of soil samples collected: 129.

Average cyst density for the field: 1·167 cysts per gm. air-dried soil.

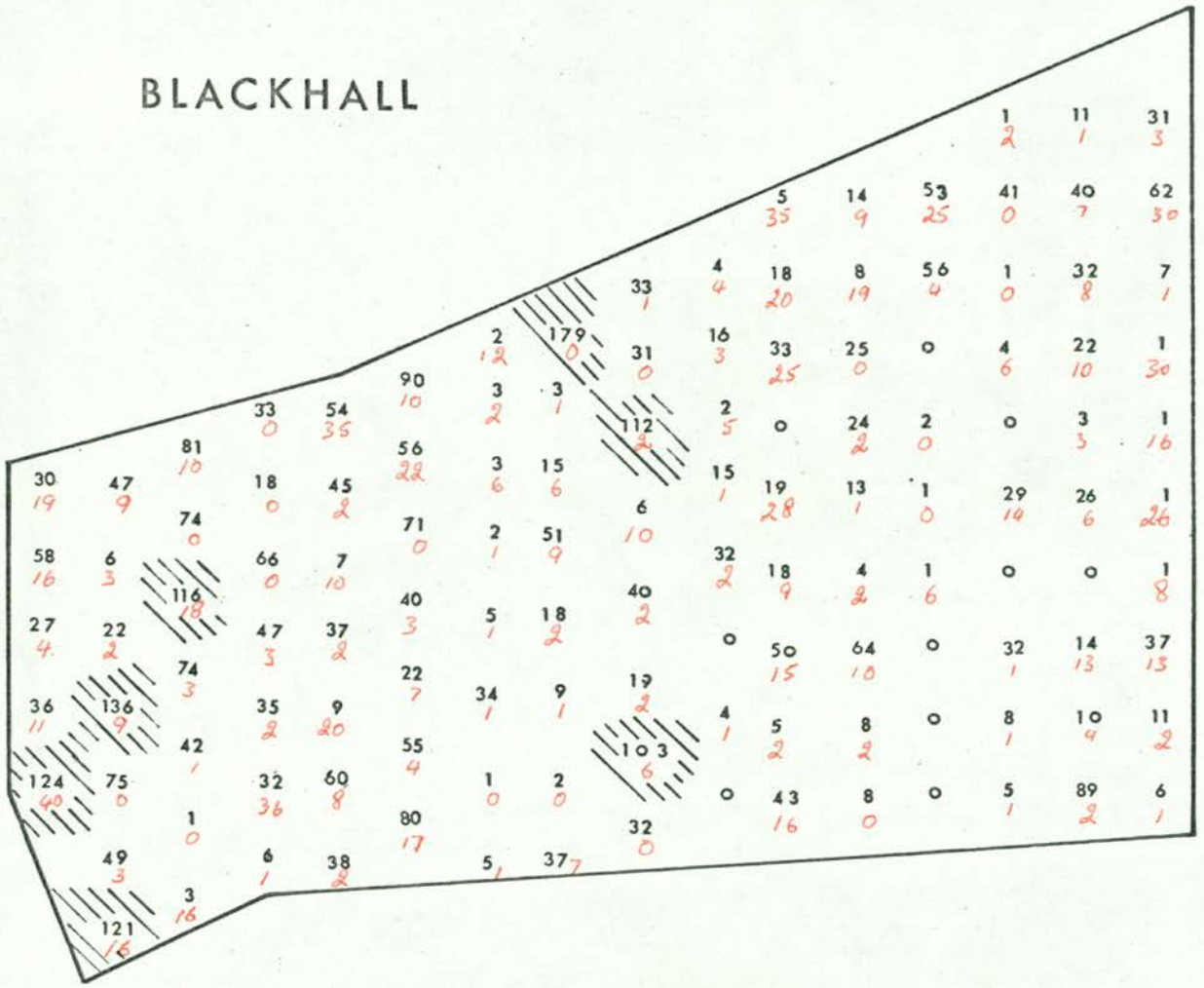
1. Ordnance Survey map, 1:25000 sheet No. NT 3031, revised edit. 1965.

2. Geological survey of Scotland, sheet No.40, 1950 edit.

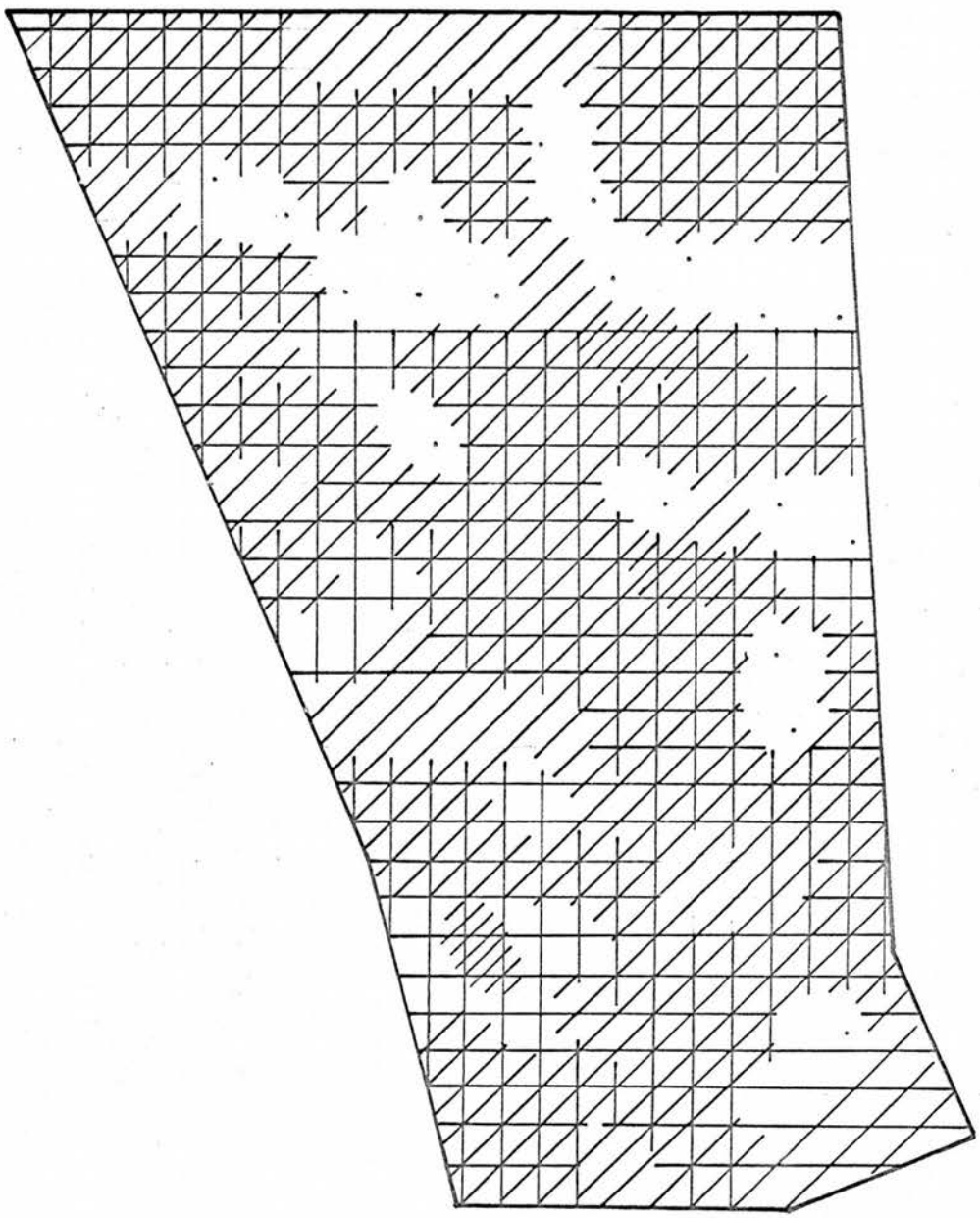
Observations: There is evidence of one principal focus of infestation and many subsidiary foci. It can be deduced from the pattern that the infested zones associated with different foci are beginning to merge. There appears to be considerable scope for further spread and increase of infestation.


BLACK HALL
N
Cysts per gram of soil
3·69-4·520
-3·680
-2·840
-2·000
-1·160
-0·800
-0·450
0·00-0·200
90 Yards

BLACKHALL


30 19
47 9
81 10
74 0
58 16
6 3
116 18
27 4
22 2
74 3
36 11
136 9
42 1
124 40
75 0
1 0
49 3
3 16
121 16
33 0
54 35
18 0
45 2
66 0
7 10
47 3
37 2
35 2
9 20
32 36
60 8
6 1
38 2
90 10
56 22
71 0
40 3
22 7
55 4
80 17
2 12
3 2
3 6
2 1
5 1
34 1
1 0
5 1
3 1
15 6
51 9
18 2
9 1
2 0
37 7
179 0
33 1
31 0
112 2
6 10
40 2
19 2
103 6
32 0
4 4
16 3
2 5
15 1
32 2
0
0
4 1
0
1 2
5 35
18 20
33 25
0
19 28
18 9
50 15
5 2
43 16
14 9
8 19
25 0
24 2
13 1
4 2
64 10
8 2
8 0
53 25
56 4
0
1 0
2 0
1 0
4 2
32 1
8 1
0
41 0
1 0
4 6
0
29 14
0
32 1
8 1
5 1
40 7
32 8
22 10
3 3
26 6
0
14 13
10 4
89 2
62 30
7 1
1 30
1 16
1 26
1 8
37 13
11 2
6 1

MAP 10,c.



BLACKHALL

Field: Blackhall.

Population grid intersection number	Number of cysts recovered in the parent population	Total number of cysts produced on Craigs Defiance S1 generation	S2 generation	H1 ex adg	Fa ex spg	H2 ex mlt	H2 ex sct	H1H2 adg x mlt	H1H2 adg x sct
1	2	3	4	5	6	7	8	9	10
1	103	31	3	0	0	10	5	-	-
2	178	62	30	0	0	8	7	-	-
3	212	7	1	0	0	0	1	-	-
4	196	1	30	0	0	11	0	-	-
5	47	1	16	0	0	3	0	-	-
6	69	1	26	0	0	2	0	-	-
7	103	1	8	0	0	10	0	-	-
8	98	37	13	0	0	4	6	-	-
9	41	11	2	0	0	3	5	-	-
10	52	6	1	0	0	8	3	-	-
11	43	89	2	0	0	3	4	-	-
12	16	10	4	0	0	3	4	-	-
13	25	14	13	0	0	7	8	-	-
14	30	0	0						
15	130	26	6	0	0	4	16	-	-
16	207	3	3	0	0	2	15	-	-
17	201	22	10	0	0	1	7	-	-
18	286	32	8	0	0	20	13	-	-
19	239	40	7	0	0	2	9	-	-
20	255	11	1	0	0	8	8	-	-
21	58	1	2	0	0	1	0	-	-
22	204	41	0	0	0	0	17	-	-
23	137	1	0						
24	134	4	6	0	0	1	25	-	-
25	88	0							
26	67	29	14	0	0	0	3	-	-
27	76	0							
28	32	32	1	0	0	7	1	-	-
29	27	8	1	0	0	3	1	-	-
30	56	5	1	0		0			
31	46	0							
32	3	0							
33	7	0							
34	10	1	6						
35	15	1	0						
36	19	2	0						
37	46	0							
38	63	56	4	0	0	8	8	-	-

Field: Blackhall (Contd.)

1	2	3	4	5	6	7	8	9	10
39	75	53	25	0	0	2	12	-	-
40	176	14	9	0	0	2	8	-	-
41	134	8	19	0	0	6	0	-	-
42	120	25	0	0	0	7	1	-	-
43	137	24	2	0	0	4	6	-	-
44	65	13	1	0	0	4	4	-	-
45	21	4	2	0	0	12	6	-	-
46	41	64	10	3	0	3	0	0	0
47	26	8	12	0	0	4	5	-	-
48	1	8	0	0	0	4	2	-	-
49	19	43	16	0	0	5	5	-	-
50	64	5	2	0	0	8	4	-	-
51	65	50	15	0	0	6	3	-	-
52	40	18	9	0	0	5	2	-	-
53	121	19	28	0	0	0	10	-	-
54	62	0							
55	66	33	25	0	0	9	2	-	-
56	88	18	20	0	0	5	10	-	-
57	40	5	35	0	0	2	23	-	-
58	8	0							
59	16	4	1						
60	54	0							
61	55	32	2	0	0	10	15	-	-
62	55	15	1	0	0	13	13	-	-
63	11	2	5	0		0			
64	35	16	3	0	0	3	12	-	-
65	64	4	4	0	0	1			
66	49	32	0	0	0	0	1	-	-
67	100	103	6	0	0	26	4	-	-
68	39	9	2	1	0	3	5	0	0
69	28	40	2	0	0	1	2	-	-
70	43	6	10	0	0	2	1	-	-
71	83	112	2	0	0	2	16	-	-
72	51	31	0	0	0	2	1	-	-
73	89	33	1	0	0	10	3	-	-
74	17	179	0	0	0	0	10	-	-
75	14	3	1	0	0	0			
76	14	14	6	0	0	3	7	-	-
77	20	51	9	0	0	14	31	-	-
78	49	18	2	0	0	3	7	-	-
79	49	9	1	0	0	3	9	-	-
80	14	2	0						
81	4	37	7	0	0	0	6	-	-
82	16	5	1	0	0	1	3	-	-
83	44	1	0						
84	57	34	1	0	0	1	3	-	-
85	95	5	1	0	0	2	1	-	-

Field: Blackhall (Contd.)

1	2	3	4	5	6	7	8	9	10
86	45	2	1	0					
87	39	3	6	0	1	9			
88	30	3	2	0		3			
89	19	2	12	0		35			
90	67	90	10	0	0	2	3	-	-
91	143	56	22	0	0	6	1	-	-
92	145	71	0	0	0	6	23	-	-
93	242	40	3	0	0	3	0	-	-
94	151	22	7	0	0	15	5	-	-
95	174	55	4	0	0	7	1	-	-
96	16	80	17	0	0	4	16	-	-
97	168	54	35	0	0	25	7	-	-
98	325	45	2	0	0	6	2	-	-
99	137	7	10	0	0	4	3	-	-
100	271	37	2	0	0	3	6	-	-
101	160	9	20	0	0	13	0	-	-
102	143	60	8	0	0	0	10	-	-
103	44	38	2	0	0	4	9	-	-
104	251	33	0	0	0	8	12	-	-
105	299	18	0	1	0	4	2	0	0
106	206	64	0	0	0	7	3	-	-
107	352	47	3	0	0	14	6	-	-
108	251	35	2	0	0	19	5	-	-
109	304	32	36	0	0	22	1	-	-
110	97	6	1	0	0	2	7	-	-
111	233	81	10	0	0	4	5	-	-
112	308	74	0	0	0	14	3	-	-
113	191	166	18	0	0	5	0	-	-
114	462	74	3	0	0	4	4	-	-
115	347	42	1	0	0	5	7	-	-
116	320	1	0						
117	161	3	16	0		36			
118	241	47	9	0	0	10	11	-	-
119	257	6	9	0	0	10	2	-	-
120	286	22	2	0	0	1	1	-	-
121	233	136	9	0	0	7	2	-	-
122	385	75	0	0	0	10	0	-	-
123	452	49	33	0	0	7	0	-	-
124	161	121	16	0	0	9	0	-	-
125	149	30	19	0	0	3	11	-	-
126	252	58	16	0	0	25	1	-	-
127	237	27	4	0	0	13	0	-	-
128	88	36	11	0	0	5	19	-	-
129	178	124	40	0	0	36	0	-	-
Means	1·167	30·12	7·76	0·06	-	3·88	4·75	-	-
Max.	4·620	179	36	1	1	36	31	-	-
Min.	0·010	1	0	0	0	0	0	-	-

Map 11a.

Field: Mount Hallow A. O.S. Number,[1] 8326.

Location: Mount Hallow, Star, Markinch, Fife.

Area: 3·243 acres.

Soil type and drainage:[2] Maundy sand and gravel, freely drained.

Height above sea level: 450 feet approximately.

Cropping history:

1960-61	Grass.
1961-62	"
1962-63	"
1963-64	Maincrop Potatoes.
1964-65	Barley.

Date of soil sampling: November, 1965.

Spacing between sampling points: 20 x 20 yards.

Total number of soil samples collected: 45.

Average cyst density for field: 2·993 cysts per gm. air-dried soil.

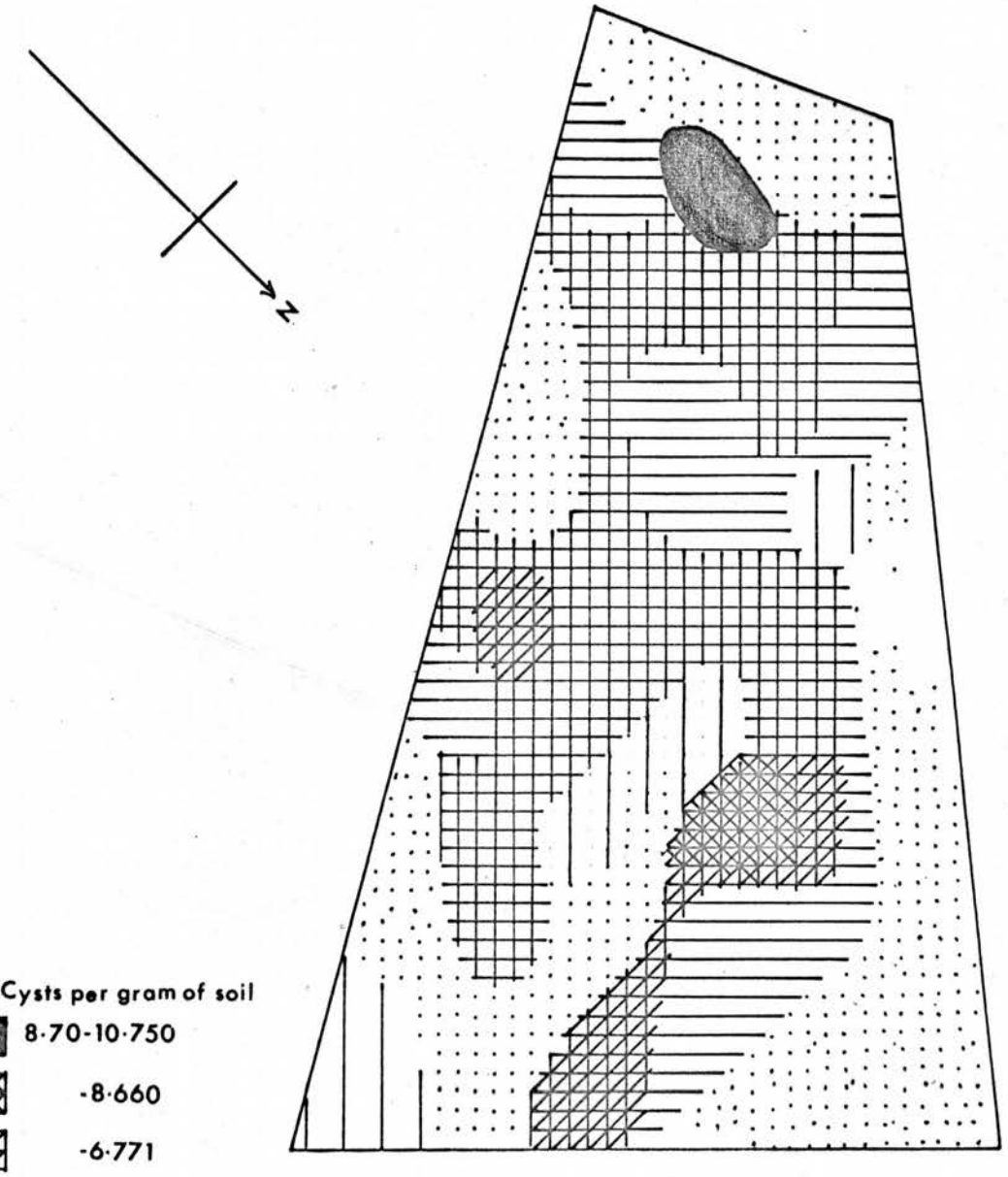
1. Ordnance Survey map 1:25000 sheet Nos. NT 3103 and 3203 Revised edit. 1965.

2. Geological Survey of Scotland, sheet No.40, 1950 edit.

Observations: There are two or three principal centres of infestation, which are not surrounded by any particular broad zone of continuous spread. The focus found near the south border of the field is very unusual, in that the area of high cyst density is surrounded by an extremely steep gradient all around, particularly precipitous to the south. Although the average level of infestation is quite high there appears to be some scope for further increase in average cyst density.

MAP 11,a.

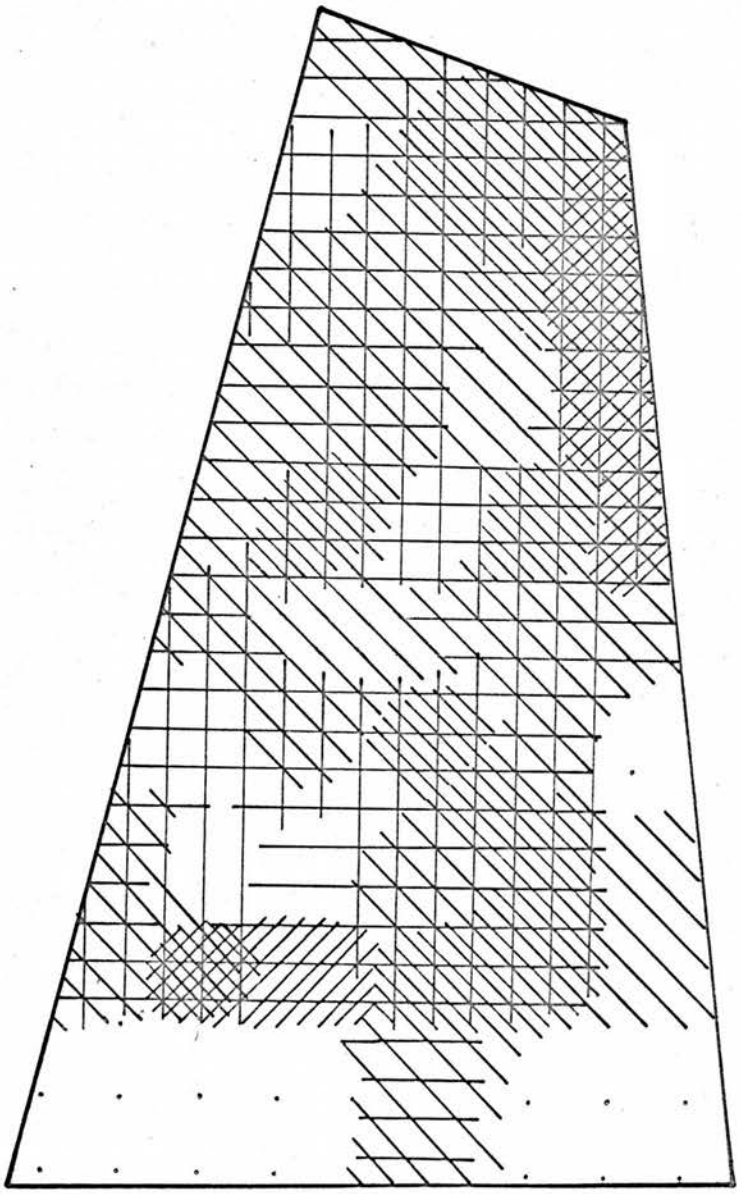
MOUNT HALLOW—A



MAP 11,b.

MOUNT HALLOW — A

MOUNT HALLOW – A



Field: Mount Hallow A.

Population grid intersection number	Number of cysts recovered in the parent population	Total number of cysts produced on Craigs Defiance S1 generation	S2 generation	H1 ex adg	Fa ex spg	H2 ex mlt	H2 ex sct	H1H2 adg x mlt	H1H2 adg x sct
1	2	3	4	5	6	7	8	9	10
1	75	1	0						
2	287	56	13	0	0	2	8	-	-
3	490	0							
4	131	3	0		0		6		-
5	195	1	0						
6	100	5	3	0		1	20	-	-
7	290	82	3	16	0	2	2	0	0
8	888	127	9	23	0	14	14	0	0
9	133	4	0		9		2	0	
10	455	26	1	1	1	10	1	0	0
11	124	10	8	0	0	1	7	-	-
12	112	61	6	0	0	14	6	-	-
13	437	5	0	0		1			
14	186	8	0	0	0	20	7	-	-
15	772	3	6	0	0	1	10	-	-
16	626	61	9	1	0	10	8	-	-
17	101	16	19	0		6	10	-	-
18	75	8	0						
19	345	5	1	0	0	6	2	-	-
20	153	19	0	1	0	1	1	-	-
21	332	2	2	0	0	1	1	-	-
22	293	4	0	0	0	11	14	-	-
23	65	9	56	0	0	8	1	-	-
24	301	18	36	0	0	4	19	-	-
25	407	9	28	0	0	10	2	-	-
26	415	3	1	0	0	0	6	-	-
27	495	49	29	0	0	12	14	-	-
28	122	37	30	0	1	4	2	-	-
29	240	65	2	1	0	24	2	-	-
30	298	6	0	0	0	13	1	-	-

Field: Mount Hallow A (Contd.)

1	2	3	4	5	6	7	8	9	10
31	555	11	14	1	0	1	3	-	-
32	146	3	18	0	0	0	2	-	-
33	110	9	1	0	0	4	4	-	-
34	255	3	3	0	0	7	1	-	-
35	377	21	1	0	0	0		-	-
36	259	3	7	0	0	11	0	-	-
37	289	23	26	1	0	10	10	-	-
38									
39	380	12	28	1	0	0	9	-	-
40	386	50	40	0	0	11	4	-	-
41	463	4	49	0	0	0	0	-	-
42	287	5	0	0	0	20	15	-	-
43	1075	37	30	1	0	3	3	-	-
44	192	45	1	2	2	6	0	0	0
45	89	5	9	0	0	0	5	-	-
Means	2·993	21·0	12·1	1·32	0·35	2·74	2·30	-	-
Max.	10·750	127	56	23	9	24	20	-	-
Min.	0·750	0	0	0	0	0	0	-	-

Map 12a.

Field: Mount Hallow B. O.S. Number,[1] 8638.

Location: Mount Hallow, Star, Markinch, Fife.

Area: 1·535 acres.

Soil type and drainage:[2] Maundy and gravel, freely drained.

Height above sea level: 450 feet approximately.

Cropping history:

1960-61	Wheat.
1961-62	Maincrop Potatoes.
1962-63	Grass.
1963-64	"
1964-65	"

Date of soil sampling: November, 1965.

Spacing between sampling points: 20 x 20 yards.

Total number of soil samples collected: 19.

Average cyst density for field: 1·866 cysts per gm. air-dried soil.

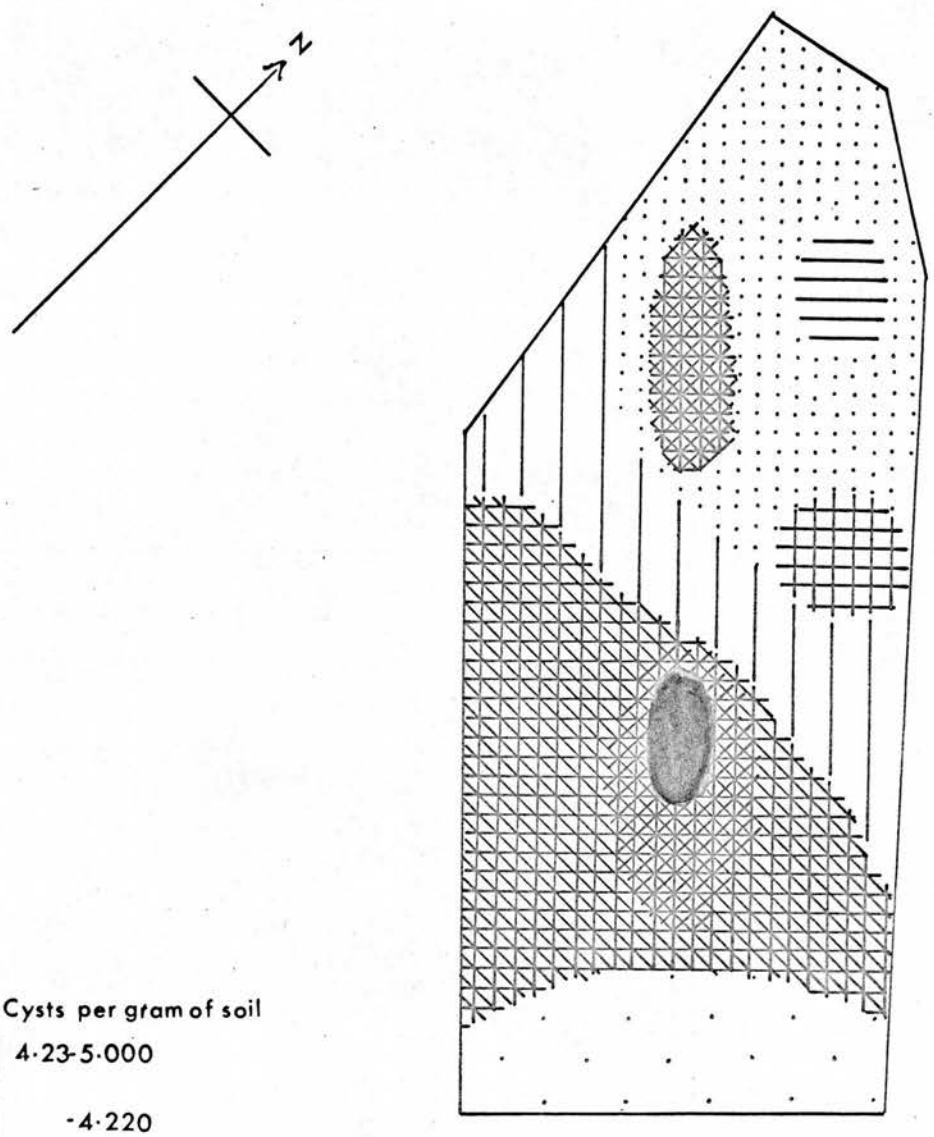
1. Ordnance Survey map, 1:25000 sheet Nos. NT 3103 and 3203 Revised edit. 1965.

2. Geological Survey of Scotland, sheet No.40, 1950 edit.

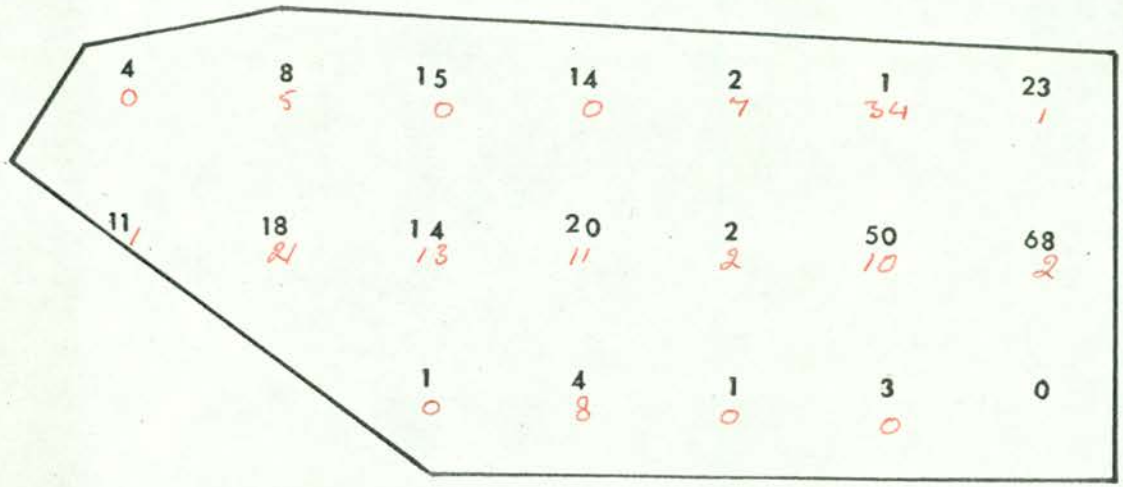
Observations: There is evidence of a primary focus of infestation surrounded by a broad zone of continuous spread, and other foci of infestation. Although the average cyst density is quite high, further spread and increase of infestation is conceivable.

MAP 12,a.

MOUNT HALLOW—B

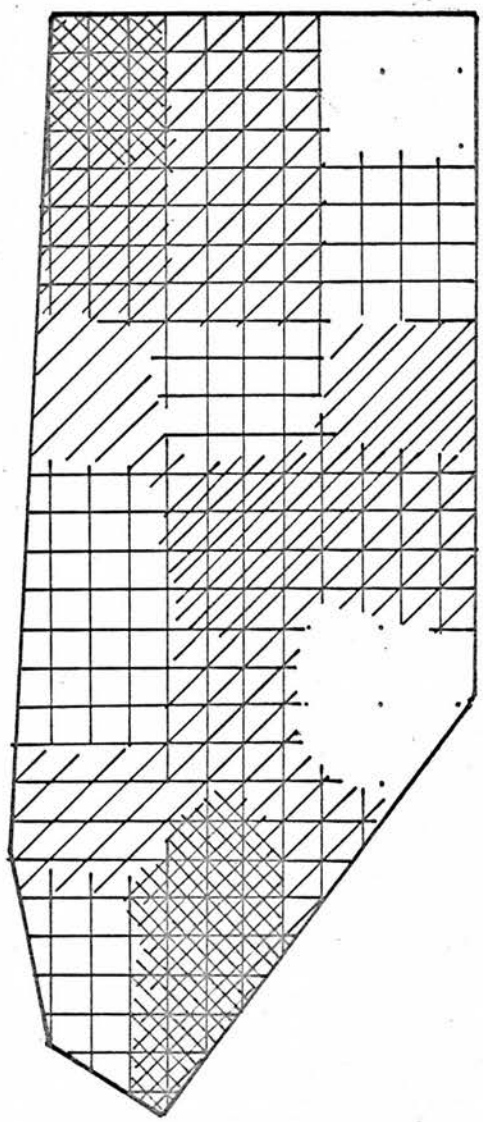


MOUNT HALLOW – B



MAP 12,c.

MOUNT HALLOW – B



Field: Mount Hallow B

Population grid intersection number	Number of cysts recovered in the parent population	Total number of cysts produced on Craigs Defiance S1 generation	S2 generation	H1 ex adg	Fa ex spg	H2 ex mlt	H2 ex sct	H1H2 adg x mlt	H1H2 adg x sct
1	2	3	4	5	6	7	8	9	10
1	1	0							
2	240	3	0	0	0	10	24	-	-
3	247	1	0	1					
4	259	4	8	0	0	20	6	-	-
5	114	1	0	0	0	4	7	-	-
6	29	68	2	0	0	7	0	-	-
7	362	50	10	0	0	10	1	-	-
8	472	2	0	0	0	10	1	-	-
9	146	20	11	2	0	2	5	0	0
10	370	14	13	0	0	0	3	-	-
11	398	18	21	1	0	1	21	-	-
12	63	11	1	1	1	1	10	-	-
13	42	23	1	1	1	5	13	-	-
14	200	1	34	1	0	11	4	-	-
15	135	2	1	0	0				
16	191	14	0	0	0	4	4	-	-
17	100	15	0	0	0	3	7	-	-
18	153	8	5	0	0	7	5	-	-
19	61	4	0	0	0	1	0	-	-
Mean	1·866	13·52	6·0	0·11	0·29	2·45	6·0	-	-
Max.	4·720	68·0	34	1	1	20	24	-	-
Min.	0·008	0	0	0	0	0	0	-	-

Map 13a.

Field: Mount Hallow D. O.S. Number,[1] 8846.

Location: Mount Hallow, Star, Markinch, Fife.

Area: 2·742 acres.

Soil type and drainage:[2] Maundy and gravel, freely drained.

Height above sea level: 450 feet approximately.

Cropping history:
1960-61 Grass.
1961-62 "
1962-63 "
1963-64 Turnips.
1964-65 Maincrop Potatoes.

Date of soil sampling: November, 1965.

Spacing between sampling points: 20 x 20 yards.

Total number of samples collected: 36.

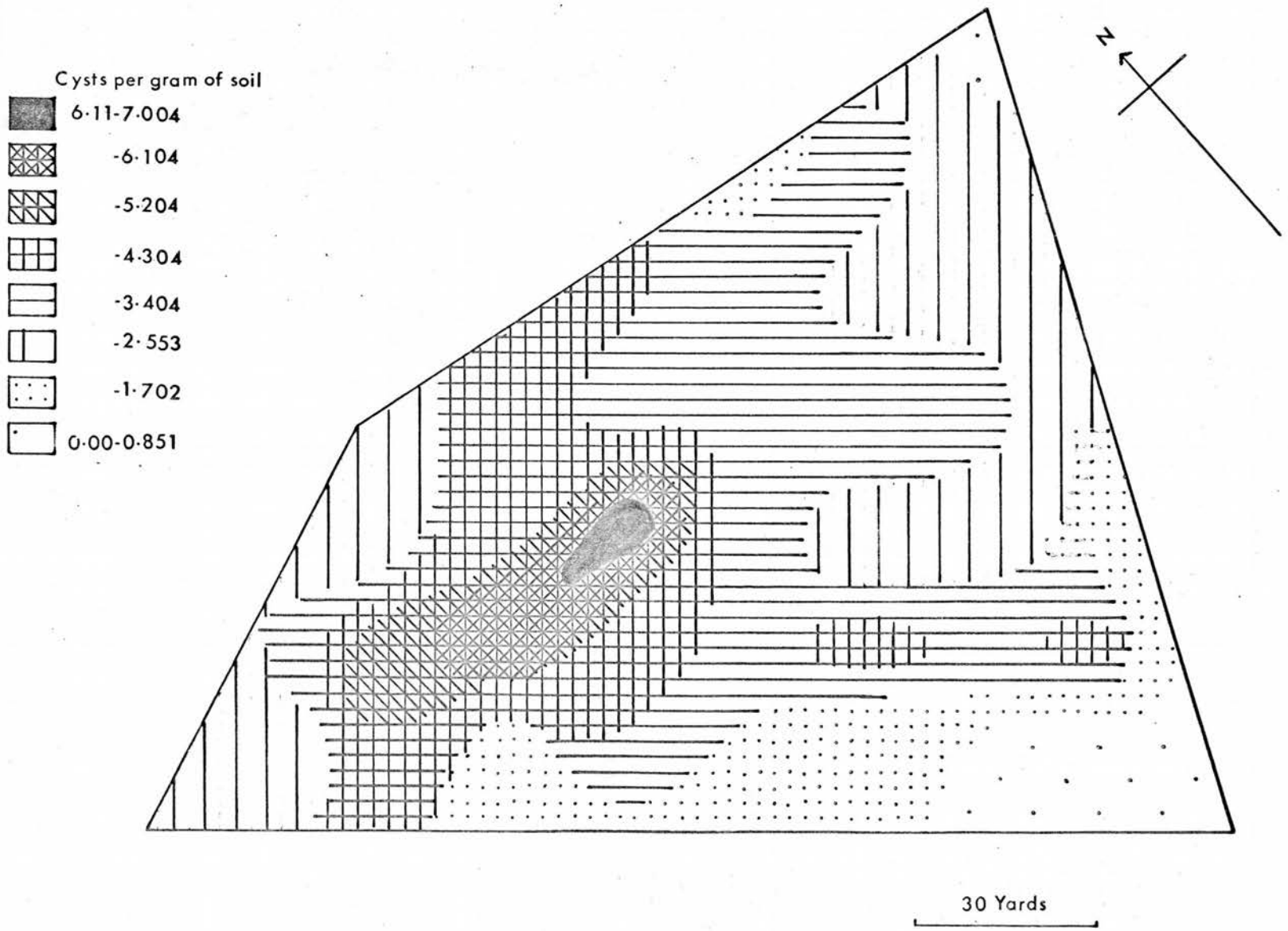
Average cyst density for field: 3·405 cyst per gm. air-dried soil.

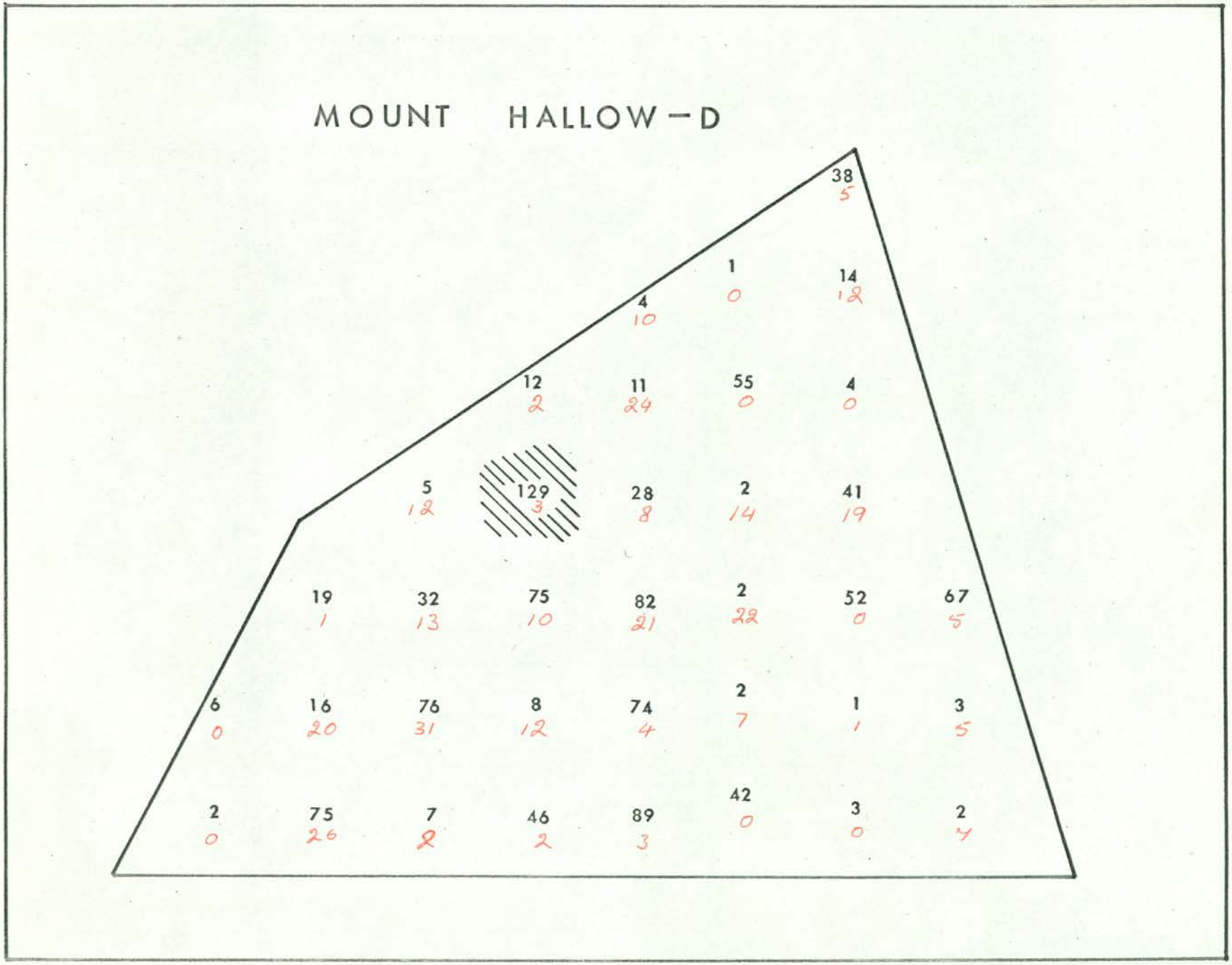
1. Ordnance Survey map, 1:25000 sheet Nos. NT 3103 and 3203 Revised edit. 1965.

2. Geological Survey of Scotland, sheet No.40, 1950 edit.

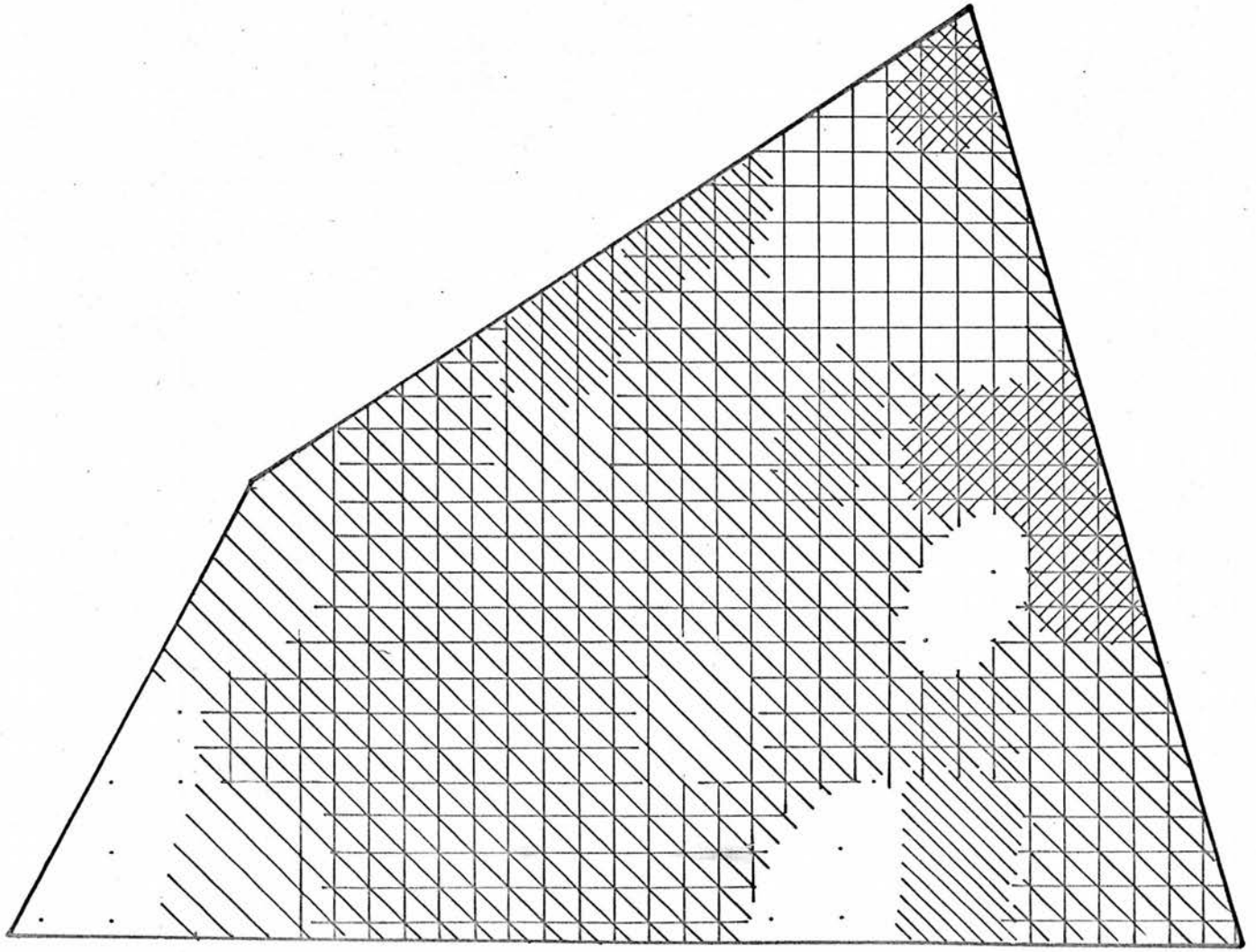
Observations: There is one principle focus of infestation which is surrounded by a broad zone of continuous spread. However, there is marked absence of any well defined zones of secondary infestation. In spite of high average cyst density, there is considerable scope for further increase in the level of infestation and simultaneous spread along a broad front.

MOUNT HALLOW—D




MOUNT HALLOW-D
38
5
1
0
14
12
4
10
12
2
11
24
55
0
4
0
5
12
129
3
28
8
2
14
41
19
19
1
32
13
75
10
82
21
2
22
52
0
67
5
6
0
16
20
76
31
8
12
74
4
2
7
1
1
3
5
2
0
75
26
7
2
46
2
89
3
42
0
3
0
2
4

MOUNT HALLOW – D



Field: Mount Hallow D

Population grid intersection number	Number of cysts recovered in the parent population	Total number of cysts produced on Craigs Defiance S1 generation	S2 generation	H1 ex adg	Fa ex spg	H2 ex mlt	H2 ex sct	H1H2 adg x mlt	H1H2 adg x sct
1	2	3	4	5	6	7	8	9	10
1	184	2	0	0	0	10	4	-	-
2	309	6	0	0	0	0	0	-	-
3	421	75	26	1	0	17	31	-	-
4	449	16	20	0	0	3	6	-	-
5	231	19	1	0	0	2	5	-	-
6	165	7	2	1	0	8	9	-	-
7	591	76	31	1	0	14	14	-	-
8	422	32	13	0	0	9	29	-	-
9	389	5	12	0	0	4	7	-	-
10	251	46	2	0	0	17	4	-	-
11	375	8	12	0	0	4	5	-	-
12	641	75	10	0	0	4	7	-	-
13	273	129	3	0	0	1	1	-	-
14	371	12	2	1	0	5	0	-	-
15	120	89	3	0	0	0	4	-	-
16	314	74	4	1	0	28	5	-	-
17	274	82	21	0	0	10	8	-	-
18	266	28	8	0	0	3	1	-	-
19	311	11	24	0	0	1	1	-	-
20	93	4	10	1	0	1	0	-	-
21	86	42	0	0	0	7	10	-	-
22	388	2	7	0	0	0	7	-	-
23	189	2	22	0	0	10	1	-	-
24	327	2	14	1	0	0	0	-	-
25	239	55	0	0	0	3	1	-	-
26	309	1	0	0	0	1	7	-	-
27	192	3	0	1	0	1	6	-	-
28	279	1	1	1	0	4	2	-	-
29	174	52	0	0	0	2	6	-	-
30	270	41	19	0	1	2	3	-	-
31	228	4	0	0	0	2	0	-	-
32	200	14	12	0	0	1	2	-	-
33	80	38	5	1	1	5	8	0	0
34	18	2	7						
35	435	3	5						
36	134	67	5	0	1	4	7	-	-
Mean	3·405	31·25	8·88	0·08	0·26	5·32	5·94	-	-
Max.	6·410	129	31	1	1	28	29	-	-
Min.	0·101	1	0	0	0	0	0	-	-

Map 14a.

Field: Mount Hallow E. O.S.Number,[1] 0049.

Location: Mount Hallow, Star, Markinch, Fife.

Area: 2·106 acres.

Soil type and drainage:[2] Maundy and gravel, freely drained.

Height above sea level: 450 feet approximately.

Cropping history: 1960-61 Barley.
1961-62 Wheat.
1962-63 Turnips.
1963-64 Maincrop Potatoes.
1964-65 Barley.

Date of soil sampling: November, 1965.

Spacing between sampling points: 20 x 20 yards.

Total number of soil samples collected: 26.

Average cyst density for field: 3·078 cysts per gm. air-dried soil.

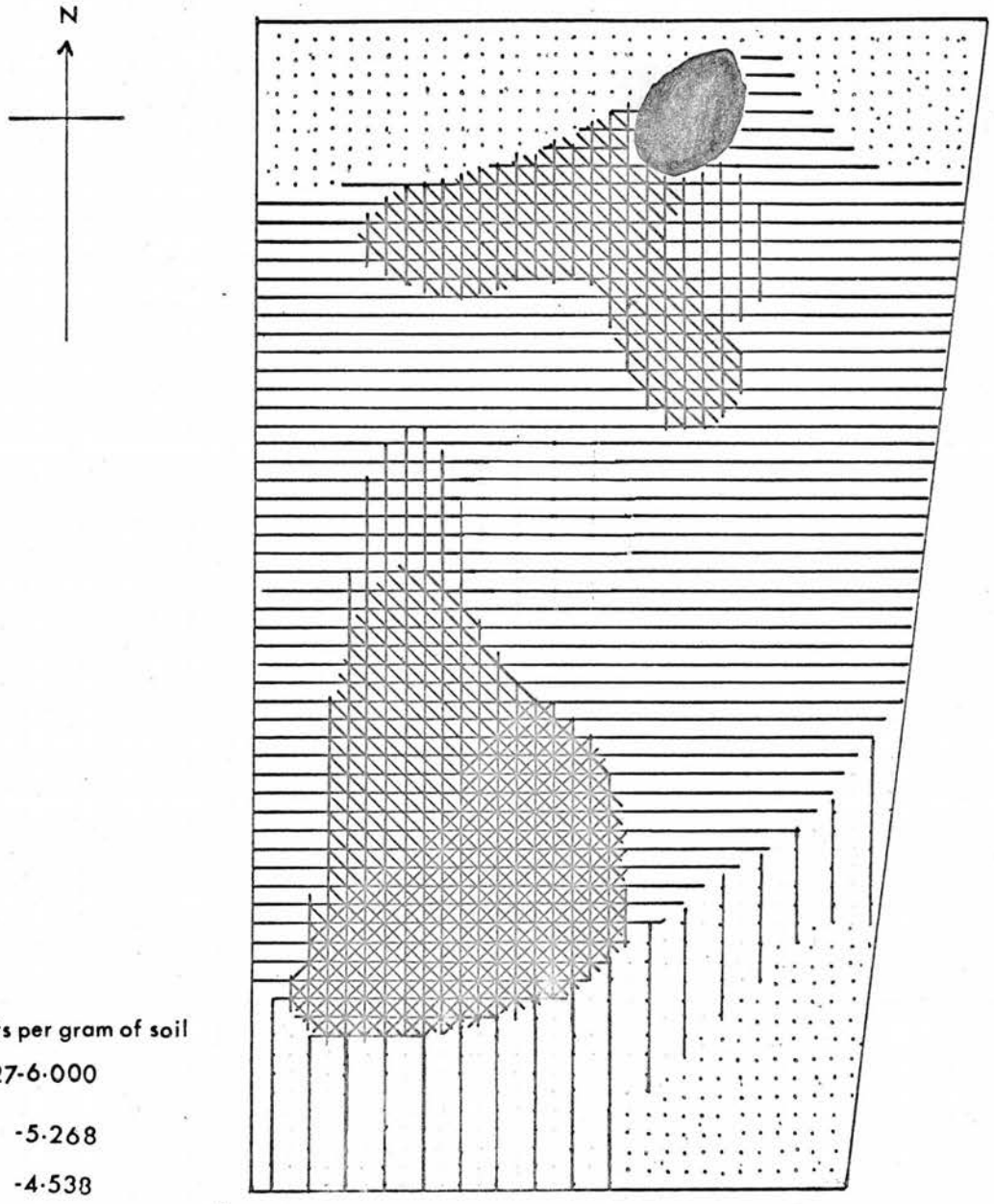
1. Ordnance Survey map, 1:25000 sheet Nos. NT 3103 and 3203 Revised edit. 1965.

2. Geological Survey of Scotland, sheet No.40, 1950 edit.

Observations: There are two primary foci of infestation, and the zones of associated continuous spread are beginning to merge. However, the unusual features about these foci are the steep gradients towards the field margins. In spite of high average cyst density, further increase and spread of infestation is possible.

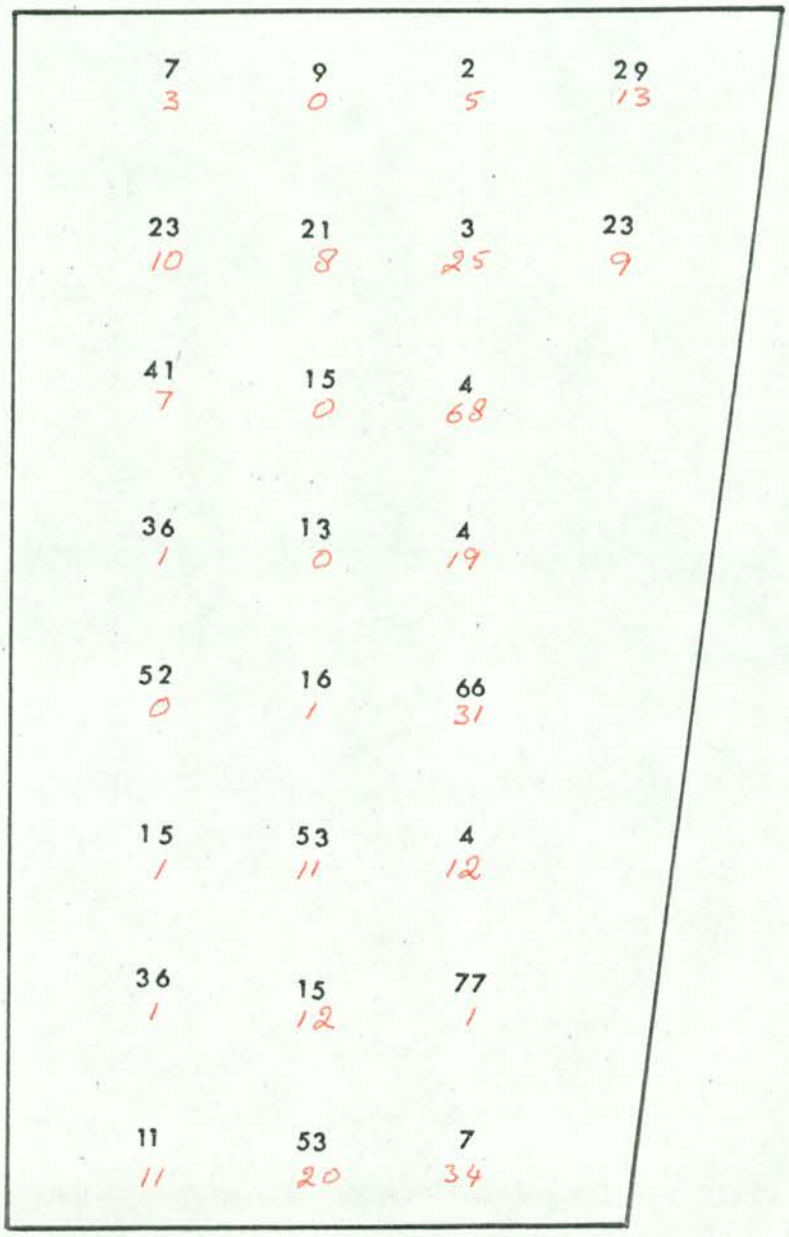
MAP 14,a.

MOUNT HALLOW—E

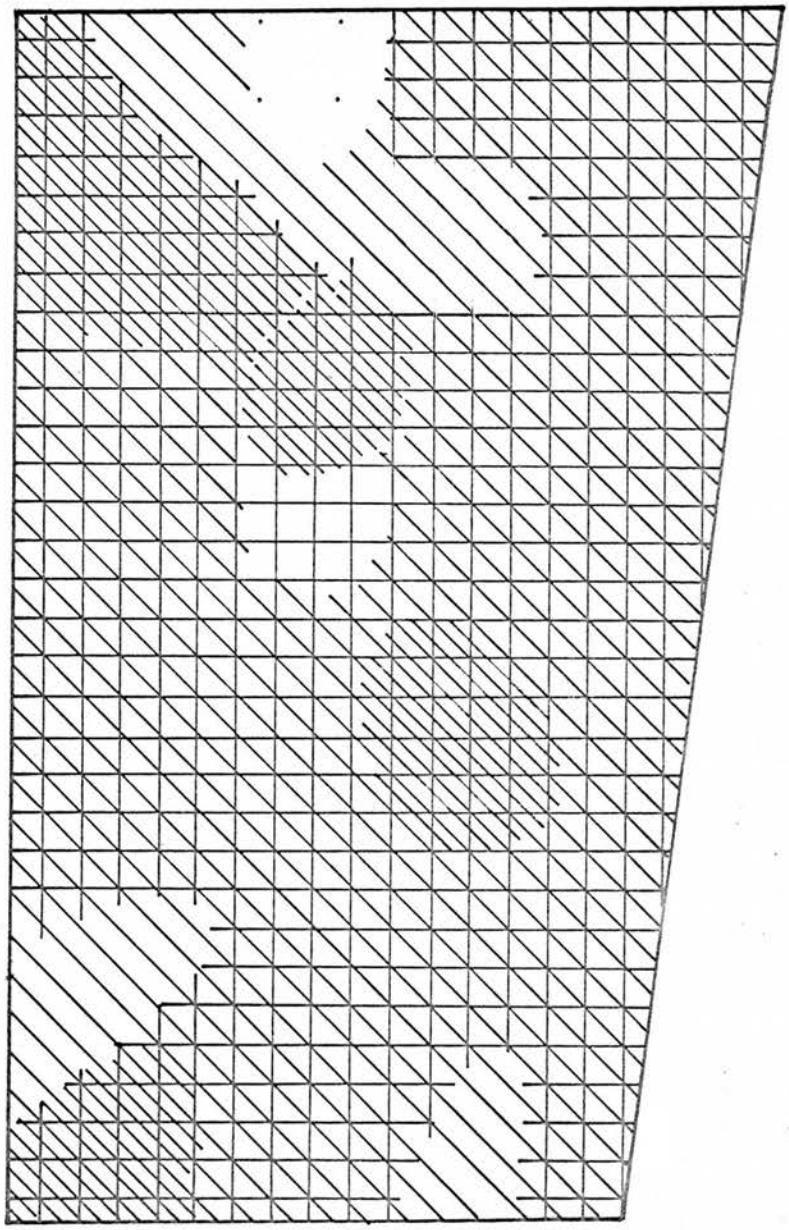


MAP 14,b.

MOUNT HALLOW—E



MOUNT HALLOW—E



Field: Mount Hallow E

Population grid intersection number	Number of cysts recovered in the parent population	Total number of cysts produced on Craigs Defiance							
		S1 generation	S2 generation	H1 ex adg	Fa ex spg	H2 ex mlt	H2 ex sct	H1H2 adg x mlt	H1H2 adg x sct
1	2	3	4	5	6	7	8	9	10
1	181	11	11	1	0	1	1	-	-
2	464	36	1	1	0	5	3	-	-
3	437	15	1	0	0	31	4	-	-
4	311	52	1	0	0	13	0	-	-
5	309	36	1	0	0	3	5	-	-
6	293	41	7	0	0	1	10	-	-
7	410	23	10	1	0	6	14	-	-
8	123	7	3	1	0	0	18	-	-
9	87	9	0	0	0	1	2	-	-
10	407	21	8	0	0	1	1	-	-
11	325	15	0	1	0	4	2	-	-
12	235	13	0	1	0	0	0	-	-
13	334	16	1	0	0	3	4	-	-
14	465	53	11	0	0	21	6	-	-
15	480	15	12	0	0	2	8	-	-
16	180	53	20	0	0	9	0	-	-
17	120	7	34	1	0	34	14	-	-
18	175	77	1	0	0	2	0	-	-
19	254	4	12	0	0	1	0	-	-
20	310	66	31	0	0	8	17	-	-
21	348	4	19	0	0	1	1		
22	404	4	68	0	0	10	1		
23	364	3	25	0	0	14			
24	593	2	5	0	0	1	1		
25	110	29	13	0	0	3	4	-	-
26	285	23	9	0	0	14	12	-	-
Means	3·078	22·4	13·1	0·26	-	7·23	5·52	-	-
Max.	5·930	77	68	1	-	34	20	-	-
Min.	0·870	0	0	0	-	0	0	-	-

Map 15a.

Field: Mount Hallow F. O.S. Number,[1] 0041.

Location: Mount Hallow, Star, Markinch, Fife.

Area: 3·480 acres.

Soil type and drainage:[2] Maundy sand and gravel, freely drained.

Height above sea level: 450 feet approximately.

Cropping history:

1960-61	Grass.
1961-62	"
1962-63	Oats.
1963-64	Maincrop Potatoes.
1964-65	Turnips.

Date of soil sampling: November, 1965.

Spacing between sampling points: 20 x 20 yards.

Total number of soil samples collected: 38.

Average cyst density for field: 2·137 cysts per gm. air-dried soil.

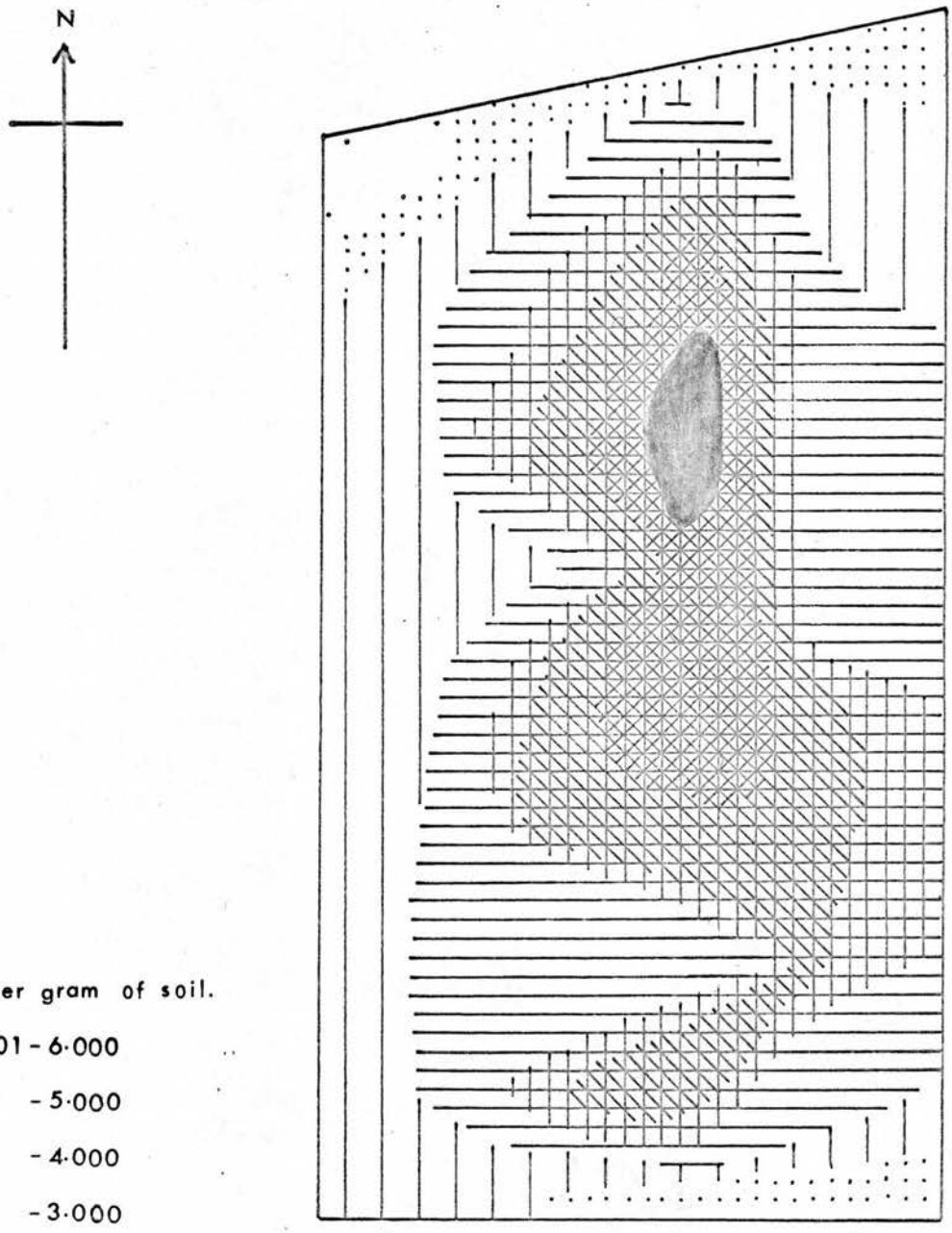
1. Ordnance Survey map, 1:25000 sheet Nos. NT 3103 and 3203 Revised edit. 1965.

2. Geological Survey of Scotland, sheet No.40, 1950 edit.

Observations: There is a single focus of primary infestation which is surrounded by a broad zone of continuous spread, extending mostly in a north/south direction, along which axis the field is also cultivated. There is a noticeable absence of any subsidiary foci. Although the average cyst density is high there appears to be considerable scope for further spread and increase of infestation.

MAP 15, a.

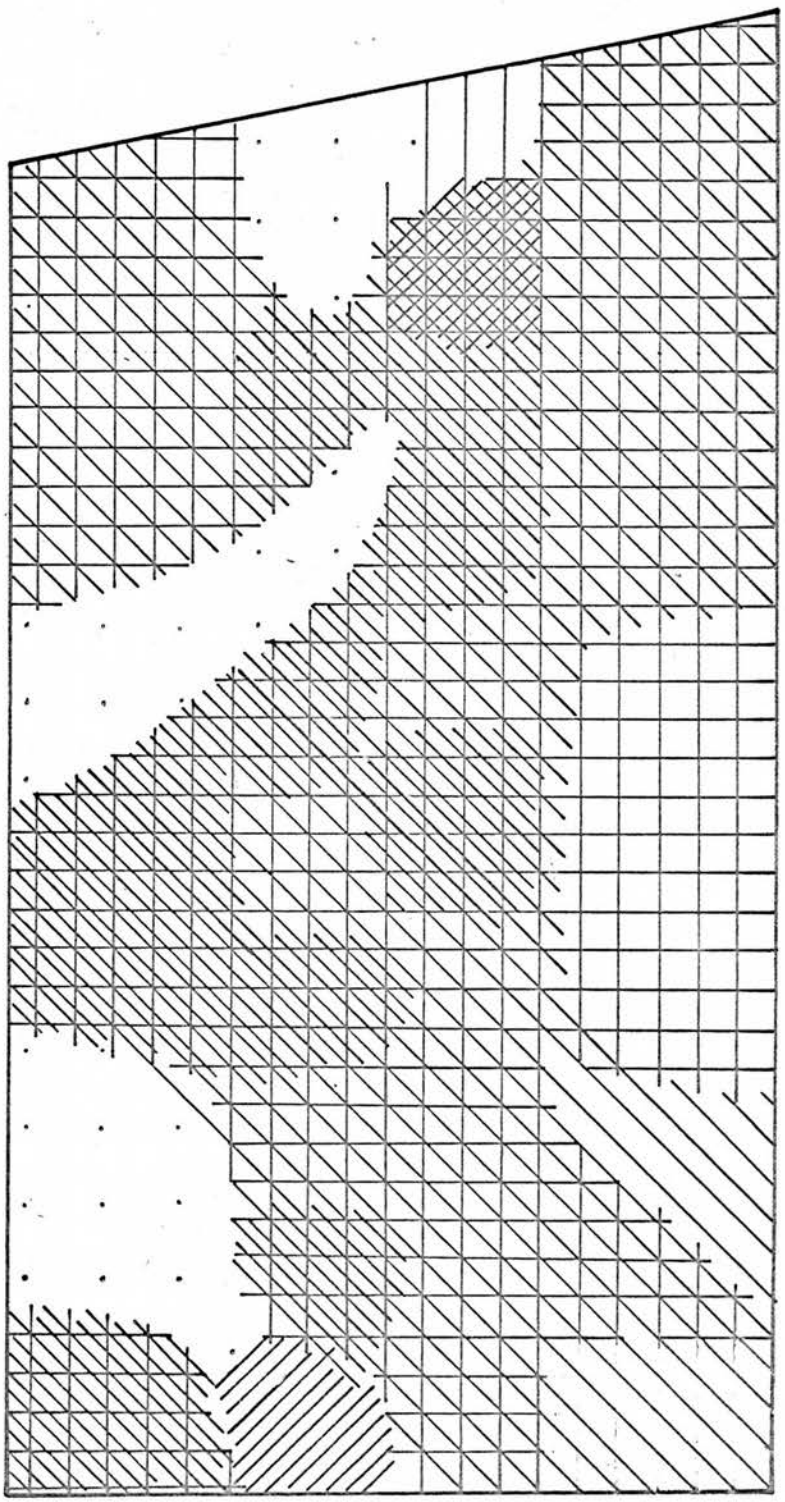
MOUNT HALLOW - F



MAP 15,b.

MOUNT HALLOW – F

MOUNT HALLOW—F



Field: Mount Hallow F

Population grid intersection number	Number of cysts recovered in the parent population	Total Number of cysts produced on Craigs Defiance S1 generation	S2 generation	H1 ex adg	Fa ex spg	H2 ex mlt	H2 ex sct	H1H2 adg x mlt	H1H2 adg x sct
1	2	3	4	5	6	7	8	9	10
1	117	6	10	1	0	2	6	-	-
2	145	1	0	0					
3	166	3	0	0	0	1			
4	173	31	5	1	0	10	10	-	-
5	129	29	7	1	0	1	1	-	-
6	107	1	0	0					
7	122	72	38	0	0	45	4	-	-
8	60	23	2	0	0	2	3	-	-
9	33	9	2	0	0	10	9	-	-
10	128	0							
11	264	67	7	1	0	9	3	-	-
12	397	0							
13	118	11	0	1	0	8	3	-	-
14	377	57	22	0	0	6	0	-	-
15	372	12	19	1	0	7	6	-	-
16	152	4	5	0	0	0	7	-	-
17	296	2	1	1	0	4	0	-	-
18	86	0		0	1	3	10	-	-
19	56	12	4	0	0	10	1	-	-
20	344	64	2	0	0	20	2	-	-
21	196	48	7	0	0	17	2	-	-
22	381	15	26	0	0	1	3	-	-
23	420	105	36	1	0	11	1	-	-
24	402	5	11	0	0	2	12	-	-
25	502	61	8	1	0	9	17	-	-
26	486	41	8	1	0	15	3	-	-
27	284	52	14	1	1	19	0	0	0
28	94	1	0	0			0		
29	71	12	4	0	0	0	12	-	-
30	102	22	13	0	0	0	0	-	-
31	149	11	1	0	0	12	9	-	-
32	198	6	6	0	0	6	0	-	-
33	156	54	4	0	0	6	3	-	-
34	243	12	0	0	0		3	-	-
35	225	8	0	0	0		4	-	-
36	263	1	0	1	0		0	-	-
37	197	4	4	1	0	1	8	-	-
38	51	3	5	0	0		7	-	-
Means	2·137	22·6	7·48	0·35	-	4·48	7·48	-	-
Max.	5·020	105	36	1	1	45	12	-	-
Min.	0·330	0	0	0	0	0	0	-	-

SECTION IV

THE RELATIONSHIP BETWEEN CYST CHROMOGENESIS AND SPECIFICITY IN POTATO CYST NEMATODE

THE RELATIONSHIP BETWEEN CYST CHROMOGENESIS AND SPECIFICITY IN POTATO CYST NEMATODE.

Introduction. Cysts of H. rostochiensis when they begin to protrude through the root cortex are always milky-white in colour; the cyst wall is soft and semi-transparent. Proteins in the wall then undergo a gradual tanning process involving polyphenol oxidase (Ellenby, 1946). As a result of this toughening process, fully mature or ripened cysts are always some shade of chestnut-brown in colour. In the transition from milky-white to brown, a yellow pigment may develop internally and impart a yellow appearance to the cyst as a whole. Guile (1966) observed that the duration of the yellow phase varied between populations. He also observed that the vivid yellow phase was characteristic of pathotype A and justified the name 'golden nematode' given to potato cyst nematode in the U.S.A. At the time of his first publication on chromogenesis, pathotypes other than A were lumped together as pathotype B, and appeared to lack the vivid yellow phase.

Consequently, frequent yellow cysts observed in the roots of a fully susceptible crop of potatoes in a certain field would suggest that the population involved was predominantly pathotype A and could probably be controlled initially by a subsequent crop of resistant potatoes, such as Maris Piper, Ulster Glade or Pentland Javelin, all of which incorporate resistance ex. subsp. andigena and are now becoming available in Britain.

Guile investigated the Duddingston population in 1967. He

confirmed (Guile in lit.) that it was a true pathotype B population according to the subsequent agreed system of nomenclature (Table 3.1.) and that it differed in cyst chromogenesis from all his other populations, which were now classed either as pathotype A or pathotype E. His results can be summarised as follows:
Pathotype A - long yellow phase, becoming vivid yellow.
Pathotype B - short yellow phase, not becoming vivid yellow.
Pathotype E - yellow phase absent or very fleeting and indistinct.

As far as British populations are concerned, the evidence available at present suggests that pathotype A invariably shows the vivid yellow phase, and the pathotype E never shows it. This means, genetically speaking that pathotype A, B and E each have two distinct and superficially unrelated characters. Pathotype A has specificity A and is 'yellow cysted'. Pathotype B has specificity B and is 'cream cysted'. Pathotype E has specificity E and is 'white cysted'.

Ford (1965) has observed that the outward manifestations of polymorphic characters are often of very trivial or superficial nature and that their significance lies in some related physiological contribution to the overall fitness of the organism. It is hardly possible to imagine a less useful character than a colour which cannot be seen while it lasts, because it develops in cysts attached to roots not exposed to light.

He also points out that the maintenance of genetic polymorphism often involves super-genes, defined by Darlington and Mather (1949) as "a group of genes acting as a mechanical unit in

particular allelic combinations".

If it could be shown that the pathotype of potato cyst nematode were governed by super-genes, then this fact, together with the already established polymorphism of specificity, should point to a classic case of genetic polymorphism.

The demonstration of super-genes in potato cyst nematode requires;

(a) the two characters distinguishing each pathotype have to be inherited together as a unit in matings between different pathotypes.

(b) In order to reveal that sets of two, more or less permanently linked genes are involved, and not single, pleiotropic genes with two effects, the detection of cross-overs is essential, although these should be rare.

Requirement (a) was not investigated in lines developed as a result of controlled matings between pathotypes because Guile's findings came too late for this work to be concluded in the time available. Instead, the now well established single cyst technique was used to analyse field populations within which matings between pathotypes might have occurred randomly in the field.

Materials. Suitable material was at hand in the form of inbred lines which had been developed from cysts kindly supplied by Officers of the National Agricultural Advisory Service, and which originated in fields or gardens in 18 counties of England and Wales. Each line comprised an S1 family of cysts produced by single-cyst

cultures on Craigs Defiance. Each field or garden came to be represented by 1-5 S1 families, depending on the number of field cysts which had reproduced.

Methods. A cyst from each S1 family was placed in a pot with each of the seven classes of potatoes already specified in Table 3.2. Root-balls were inspected and the colour of ripening cysts was recorded. The new or S2 cysts were counted after extraction by the flotation technique.

Results. The full results are presented in Table 4.1. Where cysts are enumerated in the Table with no indication of colour, it means that the cysts were not in a position to be seen on the root mat, or, if seen, were not considered to have reached the stage at which colour begins to develop.

Of the cysts in contact with Craigs Defiance, 63·86% reproduced, somewhat less than the corresponding figure of 85·35% and 87·28% recorded for the S1 and S2 generations of the Scottish populations investigated.

Two kinds of observations were considered to be diagnostic of pathotype;

(1) The production of one or more yellow cysts on any plant by at least one of the lines representing a field population suggested that pathotype A was present.

(2) The production of one or more cysts on H1H2 test plants by at least one of the lines representing a field population indicated that pathotype E was present.

White or cream coloured cysts were not considered to be diagnostic of pathotype because all young cysts are white, and cream cysts, which en masse may be characteristic of a B population, are not sufficiently distinct from white or yellow cysts in mixtures.

Field populations which satisfied criteria 1 or 2 or both are designated by appropriate symbols in Table 4.1, which also includes a few populations designated by other symbols explained in the key. The accompanying map, Fig. 4.1. shows the distribution, by county, of the nematode populations.

TABLE 4.1.

Numbers and colour of cysts produced on seven classes of potato by single-cyst lines representing English populations.

Colour of ripening cysts:

wt = white; cr = cream; yl = yellow; br = brown.

Key to population symbols:		Nematode pathotypes: A	B	E
●	Yellow cysts observed: no cysts on H1H2 plant(s), or on H1 plants	+	-	-
□	No. " " " : cysts on H1H2 plant(s)	-	+	+
◙	Yellow " " : cysts " " "	+	±	+
△	No " " " : no " " " , cysts " H1 " .	-	±	±
▲	Yellow " " : no " " H1H2 " , cysts " H1 " .	+	±	±

+ = present; - = absent; ± doubtful.

* Segregating line: yellow cysts and cysts on H1H2 plants produced by the progeny of a single cyst.

TABLE 4.1.(Contd.)

Reference number / Field	Single-cyst lines	Craigs Defiance	Class of potatoes: H1 ex adg	Fa ex spg	H2 ex mlt	H2 ex sct	H1H2 ex adg X mlt	H1H2 ex adg X sct	Population symbols
1	2	3	4	5	6	7	8	9	10
B1									
	-1	1	-	1wt	4br	-	-	-	
	-2	11	2wt	4br	4br2wt	-	-	-	
	-3*	-	-	2wt	1yl	3wt1br	-	-	
	-4*	9	21wtbr	13	1yl	-	-	-	●
	-6	6	3br	-	2	-	-	-	
	-7	-	4	8	-	-	-	-	
	-8	-	-	2	-	-	-	6	
B2									
	-11	8	5	1wt	-	-	-	1	□
B3									
	-8	6	1	3wt	4	-	-	3	□
B4									
	-2	1	8	1wt	-	-	6cr	2br	
	-3	-	-	3wt	-	-	-	2	
	-4	-	-	2	3	-	1	-	□
	-5	7	38wt	11wt	2	-	1	-	
	-6	10	1wt	18wt	-	-	-	8wt	
	-7	-	9wt6br	7wt	4cr	-	1	4wt	
B5									
	-1	-	-	5wt	-	-	-	-	
	-3*	1br2yl	-	2	-	-	-	2	◙
	-7	-	7	1	-	2	-	2	
	-8	1	12	2	5	2	-	-	
	-9	1	9	8	-	4	5	9	

TABLE 4.1. (Contd.)

1	2	3	4	5	6	7	8	9	10
B6									
	-2	-	3	-	-	-	-	-	△
	-13	-	15	10	-	-	1	-	
B7									
	-3	-	-	-	6yl	1	-	-	◙
B8									
	-2	-	14	-	4	-	9cr	4	
	-3	-	2	-	-	-	10	-	
	-5	-	3	-	1	-	11cr	1	□
	-8	1	10	-	-	-	-	-	
	-9	2	2	-	2	-	-	-	
B9									
	-5	3wt	-	5	-	-	-	-	△
B10									
	-2	-	-	6	-	-	-	-	
	-5	1	-	2	1cr	-	-	-	▲
	-7*	5	-	-	4yl	-	-	-	
DC1									
	-1	1	-	-	-	2br	-	-	
	-2*	1	3	-	7yl	1	-	-	▲
	-6	-	2	-	-	2	-	-	
	-10	3br	6	-	5	-	-	-	
DC2									
	-1	-	1	4	5wt2cr	5wt	-	2	
	-3	9	-	-	8	2br	1	-	◙
	-4*	8	-	-	15ylbr	-	1	-	
	-5*	25yl	-	-	5yl	27	1	-	

TABLE 4.1. (Contd.)

1	2	3	4	5	6	7	8	9	10
DC4									
	-2	3	-	14	-	-	-	1	⊡
	-4	1	-	2	-	-	-	1	
	-6*	3	-	1	5br	-	-	-	
DC5									
	-5	8	-	-	4yl	9br	-	-	
	-6*	-	-	-	10yl	4	2	-	•
	-9*	-	-	-	8	2yl	-	-	
DC6									
	-1	2	-	5cr	-	-	-	1br4wt	
	-2	4cr	-	1cr8br	2	1	-	3cr	□
	-3	29	3br1cr	10br	11	-	-	3cr1br	
DC7									
	-3	-	-	-	-	-	5	-	
	-8	4	-	-	15yl	-	-	-	⊡
	-9*	7yl	-	-	5yl	5	-	1	
DC8									
	-3	1	-	-	-	2	-	-	•
	-4	4yl	-	-	-	2	-	-	
DC10									
	-1	-	-	3wt	-	-	-	-	
	-3	-	12wtbr	3wt	3	3wt	-	-	
	-4	-	8wtbr	-	4	2	6	4	□
	-5	1wt	1wt	1	-	3	3	-	
	-6	16	10wtbr	8wtbr	-	-	-	-	
W01									
	-3	-	-	-	-	2	-	2	
	-7	78y1br	-	-	26	2yl	-	-	⊡
	-9	35	-	-	3	2	-	-	

TABLE 4.1. (Contd.)

1	2	3	4	5	6	7	8	9	10
WM1									
	-1	19cr	-	4	1cr	-	-	-	
	-2	13	4cr	6br	4cr	5	3	2wt	□
	-3 *	40cryl	3cr	-	9	-	1	9	
	-4	11	1	7	-	-	-	-	
	-5	3	4cr2wt	6	-	1	-	3	
	-6	8cr	1	1	3	-	-	-	
WM2									
	-1	6wt2br	-	2	-	-	-	-	□
WM4									
	-4	2	-	-	-	-	-	-	Δ
WM5									
	-2	1	2	-	-	-	-	4wt	
	-3	7	4	-	-	-	-	-	
	-4	20	3wt11br	2	3	-	2	1wt	
	-5	31	20wtbr	5	9	-	-	4wt2br	□
	-6	-	-	5br	-	-	-	-	
	-8	-	2	-	-	-	5wtbr	1wt	
	-9	1	7	3	2	-	-	2wt	
WM6									
	-1	-	-	4	2	-	-	-	
	-6	3	-	5	2wt	-	-	4	◙
	-8*	1	2	-	3	1yl	-	-	
BST1									
	-3	3	-	-	2	-	-	3	
	-4	2	3wt	-	-	9	-	3	□
	-6	1	-	-	8	12	-	-	
	-7	1	4wt	-	-	-	-	2	
BST2									
	-2	2	2	-	-	-	-	-	□
	-3	-	-	1	-	-	-	2	
	-7	12	-	-	-	10	-	-	

TABLE 4.1. (Contd.)

1	2	3	4	5	6	7	8	9	10
HL1									
	-1	-	8wt8br	-	-	-	-	-	
	-3	-	-	-	-	-	2	3	
	-5	-	-	-	-	-	4wt2br	-	□
	-6	-	6	-	2cr	-	3wt	3	
	-10	33	7	6	-	3	3wt	3wt	
HL2									
	-3	4	-	-	5	-	9	4	□
	-7	4	2wt	3	-	-	5	9	
HL3									
	-5	3wt	-	-	2	-	-	2wt	□
HL4									
	-3	-	-	1	1	3	-	-	△
DUR2									
	-2	-	-	-	-	-	-	5wt	□
	-7	-	1	-	2	15	-	2	
DUR3									
	-1	3	-	-	1	-	3	1wt4br	
	-3	1	-	-	1	2	-	-	
	-5	11wt	1	-	-	3	4wt	-	□
	-6	3	-	1	9wt	2	-	2	
	-7	12wt	-	-	-	-	-	3	
CUM1									
	-4	30y1br	-	-	2	1	-	-	•
	-9	18y1	-	-	5y1	-	-	1y1	
WES2									
	-1	4	1	-	-	-	2	-	
	-2	-	-	5wt	8	-	-	-	
	-3	11	-	9	-	2	7	1	□
	-4	7	8wt	-	4wt	2	4	11	
	-5	3	4wt	-	-	2	4	-	
	-6	16	3	-	-	9wtbr	2	2wt	

TABLE 4.1. (Contd.)

- 1	2	3	4	5	6	7	8	9	10
NOR1									
	-1	-	1	3	-	-	-	-	
	-2	-	1	-	8	1	-	-	◙
	-4*	4yl	3	1	2	2	-	1	
	-9 *	2yl	2	-	-	-	-	-	
NOR2									
	-2	6	-	-	-	-	2wt	-	
	-6	6wt	3	9	-	-	-	-	□
	-7	-	5	-	-	-	1	8	
NOR3									
	-2	-	-	3	2	-	1wt	-	
	-3 *	2	3	-	4yl	4	3wt	-	◙
	-4	12	3	8wtbr	3wt	3	-	2wt	
	-5	-	-	-	11	-	-	24	
	-6	-	8	-	-	-	-	-	
YL1									
	-4	12	6	1	3wt	-	2wt	21wtbr	□
	-7	15wtbr	-	-	1	3	-	1	
YL2									
	-1	5	-	5wtbr	4	-	-	4wt	
	-5	-	-	5wtbr	7	-	-	-	□
	-6	12wt	-	5br	4	1	-	17	
	-8	-	11	-	3wt	-	-	2	
	-9	13wtbr	-	-	2	-	-	2wt	
YL3									
	-4	3	1	1	2	-	10	3	
	-5	10	-	-	9wtbr	-	2wt	1	□
	-8	-	-	-	2wt	-	-	-	
YL4									
	-3	3wt	-	-	3yl	-	-	-	●
	-4	-	-	-	4yl	-	-	-	

TABLE 4.1. (Contd.)

1	2	3	4	5	6	7	8	9	10
YL5									
	-2	2	3	5wtbr	-	-	1	3	
	-3	3	4	1wt	-	3	2	24	
	-4	6	-	4wtbr	4	2	-	4wtbr	□
	-5	1	-	1	6	-	-	-	
	-6	1	-	3wtbr	5wt	-	-	5	
	-7	-	6	3wt	10br	-	-	2br	
YL6									
	-4	30br	10wtbr	7	1	1	1	6	
	-5	9	1	5	4	-	2	12	
	-7*	6yl	-	4	16	-	1	-	◙
	-9	14wt	-	6	8	-	1	4	
	-10	-	-	1wt	3	-	-	-	
YL7									
	-2	5wtbr	5	3	-	-	-	-	□
	-5	10wtbr	3br	-	-	-	-	-	
YL8									
	-3	2	3wt	1	1	-	-	1	
	-4	-	-	1	1	1	3	-	
	-5	10	-	2	-	2wt	-	-	□
	-6	-	-	3	4br	-	-	-	
	-7	2br	1	9	6wt	-	5	-	
	-8	12br	2wt	1	6wt	-	4	2br	
YL9									
	-1	10	7	-	-	-	-	-	
	-2	25	7wtbr	10	15wtbr	2wt	4	3	□
	-3	-	3wtbr	-	-	-	3	-	
	-5	6wtbr	1wt	21	4wtbr	1	-	-	
	-6	16wtbr	2	3wt	2wt	1	-	18	
	-7	35wtbr	12wtbr	12wtbr	2	3	8	-	
	-8	33br	3wt	5br	1wt	-	6br	-	
	-12	2wt	2wt	-	-	-	-	3	
	-13	5	23wtbr	5	-	-	-	6wtbr	

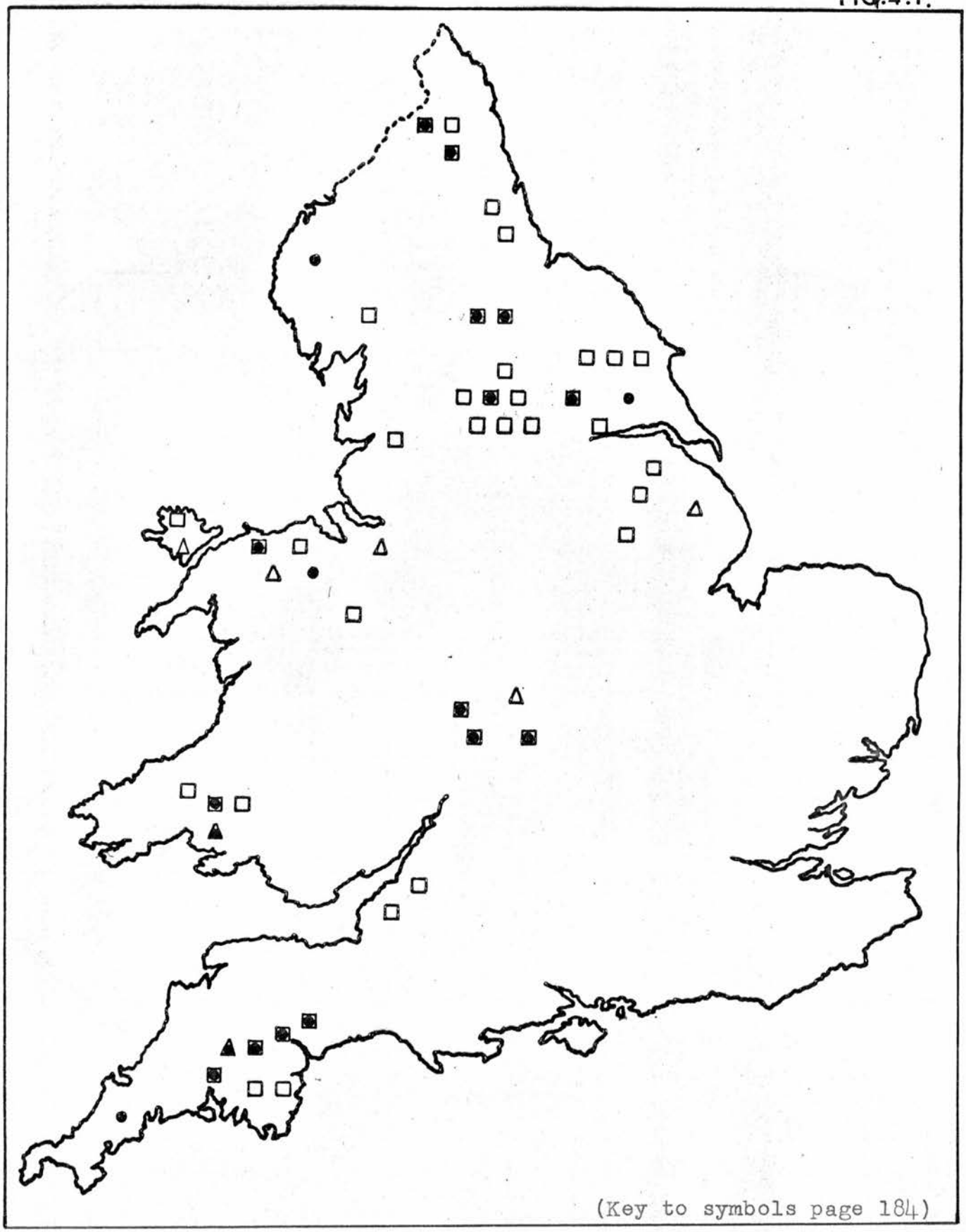
TABLE 4.1. (Contd.)

1	2	3	4	5	6	7	8	9	10
YL10									
	-2	-	5	4wt	-	1	1	6br	
	-3	6wtbr	3br	-	-	-	-	-	□
	-5	14br	5	-	-	1	-	3br	
	-6	-	1	13br	1	-	-	-	
	-9	-	-	1	2	3wtbr	-	3	
YL11									
	-2	-	2	-	1	-	-	3	
	-7	3	3br	3	2	-	-	-	□
	-8	2br	19	6	2br	2	-	-	
	-9	2br	3br	1	2	-	1wt	3br	
YL12									
	-1*	-	5wtbr	-	-	2yl	2	2wt	
	-2	4	2	2	8	-	-	-	
	-3	-	1	-	3	-	-	-	◙
	-4	1	-	1	6br	7	-	-	
	-5	1	2wt	5br	4	8	-	2	
	-8	6	-	3	-	1	-	1	
YL13									
	-1	29wt	-	-	6	-	1	5br	
	-2	3	3wt	6	-	3wt	-	-	
	-3	1	-	-	-	-	-	3wt	
	-4	-	-	9br	-	6	1wt	2br	
	-5	-	-	-	-	11	-	-	□
	-6	33br	5wtbr	5	3	1	1	-	
	-7	16br	3br	-	8	1	-	1wt	
	-8	-	-	-	-	-	-	5br	
	-9	-	-	-	-	-	-	2br	
	-22	-	-	1br	-	-	-	4wtbr	
	-24	-	-	-	-	1br	-	2br	

TABLE 4.1. (Contd.)

1	2	3	4	5	6	7	8	9	10
YNR2									
	-2	4yl	-	2yl	2	1	-	-	◙
	-5	-	4wt	7wt	3	3	2		
	-6	-	2wt	-	2	-	-	1wt	
YNR3									
	-4*	11yl	-	-	2	-	-	1	
	-5	12	-	-	-	-	-	3	◙
	-6	-	-	1wt	-	-	1	2	

FIG.4.1.



Distribution of the field populations listed in Table 4.1.

Discussion.

The inheritance of colour and specificity.

Yellow cysts were recorded on a total of 35 plants, including 14 recessive plants (Craigs Defiance) and 19 which had the H2 gene, one which had the gene Fa, and one which had combined H1H2 genes. Therefore all but two of the records of yellow cysts were on plants susceptible to pathotype A, which agrees with Guiles' observation that yellow cyst colour is typical of pathotype A.

The question now is why should specificity A and the yellow-cysted character usually be inherited together and, similarly, why should specificity E and the white-cysted character be inherited together? Are these pairs of characters truly linked in H. rostochiensis or are they simply fixed characteristics of two subpopulations which do not interbreed?

It can be seen from Table 4.1. that some 14 field populations comprised a mixture of pathotype A and E on the basis of criteria 1 and 2, some 16 lines derived from 13 of these populations individually satisfied criterion 1 and 2 and are denoted by asterisks in the Table. Since any individual line comprised of a family of S1 cysts produced by sibmating within the progeny of a single field cyst, this is conclusive evidence that pathotype A and E interbreed to some extent, in which case specificity and cyst colour must be controlled by pairs of genes which are linked, possibly so closely that each pair constitutes a super-gene.

The two definitely yellow cysts which were seen on one Fa plant ex spg and the single yellow cyst seen on H1H2 plant

ex adg X mlt were exceptional and could be explained in a variety of ways, such as:

(a) Occasional individuals of pathotype A may encyst in H1 plants despite the resistance operating against them.

(b) Occasionally individuals of pathotype A may encyst in sections of root in which the resistance is not operative, possibly due to mutation in the root, or due to some physiological disturbance however caused.

(c) Possibly the yellow-cysted individuals which occasionally encysted on the roots of H1H2 plants were the results of a rare cross-over between the members of a super-gene; they could be yellow pathotype E.

This leaves considerable scope for further investigation, since the mechanism of inheritance of specificity E has yet not been investigated. Some research along these lines seems to be necessary, since pathotype E is probably as frequent as pathotype A in English populations judging from Fig. 4.1. The pathotype B remains obscure, because it tends to be masked by pathotype E.

GENERAL DISCUSSION: Balanced polymorphism in parasitic systems.

In the supplement on Advancement of Science, published in Nature 1967, certain topics were selected for discussion because they had excited special interest in the preceding year or so. One of these was, "Intensive selection and the speed of evolution". It was concluded that the conditions for rapid evolution are fulfilled more often than had been supposed.

The conditions under which evolutionary changes proceed fast enough to be detected and analysed by observation and experiment were stated by Ford (1965) to be:

(a) Small size of population.

(b) The existence of two or more forms of the same species within the same habitat.

(c) Great selective advantage of a character.

These conditions can all be satisfied in H. rostochiensis, for the following reasons.

(a) In the initial stages of colonization of a field, populations are small and isolated: in the extreme case, a whole field population may be descended from the progeny of a single founder cyst, an idea supported by the patterns of population density discussed in Section 1.

(b) Two or three interfertile, polymorphic, colour-phases or forms coexist as distinct pathotypes in varying frequencies in many fields, as established in Sections II and III.

(c) In a crop of resistant potatoes growing in infested land, the corresponding resistance-breaking character is more than highly

advantageous in the nematode population; it is essential for regeneration.

It follows that the prospect of using strain-specific resistance to achieve lasting control of even a single field population of H. rostochiensis is probably remote. Some temporary degree of control over the period of a few rotational cycles is probably the best that can be hoped for. There may be a better prospect of obtaining lasting control by means of generalised, polygenic resistance, but this is not a subject which is pertinent to the thesis.

Prospects apart, it seems fair to say that the pathotypic variation in H. rostochiensis is extremely interesting from the standpoint of view of ecological genetics. In the 100 years or more which are presumed to have elapsed since the potato cyst nematode was first introduced into Europe from South America, probably about the middle of the nineteenth century (Jones, 1966), its specificity genes almost certainly found no expression in resistance-breaking, because there is reason to believe that none of the varieties grown in Europe before 1960 possessed strain-specific resistance. It follows that the specificity genes were probably associated in some way with the overall viability or fitness of potato cyst nematode in its spread and multiplication on potatoes lacking major resistance genes. In support of this contention, certain experimental evidence presented in Appendix 2 suggests that pathotype B is less fit than pathotype A in its multiplication on potatoes lacking resistance genes, and this fact

was seen to be consistent with the pattern of distribution of pathotype B in field populations which were predominantly pathotype A.

Therefore, the continued persistence of pathotype B in competition with pathotype A, over many generations produced in potatoes lacking resistance genes, requires some explanation. It was established (Appendix 2) that specificities A and B are governed by two alleles such that VaVa or Vavb gives specificity A and vbvb gives specificity B. This opens up the possibility that vb could be maintained by heterozygous advantage at a frequency considerably greater than could be maintained by recurrent mutation; but the really striking advantage of such an arrangement would lie in the fact that a certain balance between vb and Va could now be maintained indefinitely in potatoes lacking resistance genes. This reduces specific resistance breaking to a secondary function of the genes vb and Va, but an extremely important function in certain circumstances, permitting rapid adaptation in populations coming in contact with a host incorporating a specific resistance gene.

In the course of adaptation, a pre-existing balance between specificity genes will certainly be altered, but probably not to the extent that one specificity gene becomes fixed and the other lost, because specificity is not as important in males as in females. Males can emerge from plants in which the encystment of females has been almost completely suppressed.

Therefore, since there seems to be fairly elaborate provision

for balance between pathotype A and B, having the advantage of promoting flexibility of response to resistance in the host, it is open to speculation that the frequency of pathotype E, relative to the frequencies of pathotype A and B, can also be balanced to some extent in populations. Pathotype E is certainly polymorphic in H. rostochiensis, probably about as frequent as pathotype A (Fig. 4.1.) and interbreeds with pathotype A, judging from the segregation of characters in some of the single-cyst lines discussed in Section III. The mechanism of inheritance of specificity E has still to be established, however, before a genetic basis for balanced polymorphism of pathotypes A, B and E can be fully confirmed.

It has already been established that polymorphism of specificity is linked with polymorphism of cyst colour; the three pathotypes can be described as polymorphic colour-phases of H. rostochiensis. The significance of cyst colour probably lies in its linkage with specificity, or the linkage of specificity and some factor associated with colour, since the transient differences in cyst colour cannot be seen underground.

It is noteworthy that allelomorphic super-genes controlling groups of superficially very distinct characters are frequently concerned in the maintenance of balanced polymorphism in populations.

It is generally accepted, that the advantage inherent in balanced polymorphism is that when the success of a population in a particular environment is related to a certain balance between the frequency of different alleles, then this balance can very easily and rapidly be adjusted in response to even minor changes

in the environment.

The relative frequencies of the yellow 'cysted' and white 'cysted' forms of H. rostochiensis have not as yet been studied in relation to many of the environmental factors which may vary from field to field, but there are indications that yellow cyst colour predominates in rather special situations. Such examples are to be found in the early potato growing fields of East Lothian and Ayrshire, where there could be selection for a shortened life cycle, and in the black-fen areas of Lincolnshire.

It is possible that if the balance between the polymorphic forms were upset for no reason other than founder effect, a trend towards restoration of equilibrium in succeeding generations might be expected. Any such trend would make the oldest populations of H. rostochiensis the most difficult to control by means of strain-specific resistance.

The oldest established populations are probably South American populations, about which little is known except that the only one which appears to have been investigated so far broke the resistance of subsp. andigena (Van der Laan and Huijsman, 1957). The oldest populations in Europe are possibly those in the vicinity of Rostock, near the Plant Breeding Station at Gross-Lüsewitz (East Germany), where potato cyst nematode was first identified (Zimmermann, 1914), and these have proved extremely difficult to control by means of varietal resistance (Stelter, 1961). The oldest populations in England are possibly some of those occurring in the East Midlands and further North, as the parasite was first detected near Hull (Strachan and Taylor, 1926). In these regions

it has been established by officers of the National Agricultural Advisory Service that resistance ex adg or mlt, and ex adg X mlt is likely to be less useful than elsewhere.

The advantages of polymorphism in a parasite are obvious enough to have attracted considerable discussion in the past.

Mode (1958) analysed a model system involving specific interactions between two R alleles in the host and two separate loci in the pathogen, and concluded on mathematical grounds that such a system would, under certain conditions, eventually reach a stage of equilibrium. Subsequently Person (1966) suggested that the commonly observed features of parasitic systems should be viewed in terms of the theory of balanced polymorphism (Ford, 1964). It appears that whenever a gene for gene relationship between host and parasite has been established or suggested (Table 3) the resistance genes (R genes) are dominant and commonly allelic, while the specificity genes (or V genes) are recessive and show no evidence of allelism. On the basis that the frequencies of R genes and V genes are interdependent, Person suggested, in effect, that a cycle in the frequency of R genes set up a related but out-of-phase cycle in the frequency of V genes. He drew up a model showing how R genes could become polymorphic in the host and V genes polymorphic in the parasite.

TABLE 3.

Parasitic systems in which gene for gene relationships have been reported or suggested.

System	Author(s)	Year.
Linum and *Melampsora*	Flor	1955
Solanum and *Phytophthora*	Toxopeus	1956b
Lycopersicum and *Cladosporium*	Day	1956
Malus and *Venturia*	Boone and Keitt	1957
Hordeum and *Erysiphe*	Moseman	1959
Triticum and *Erypsiphe*	Powers and Sando	1960
Triticum and *Puccinia*	Zadoks	1961
Triticum and *Tilletia*	Metzger and Trione	1962
Triticum and *Puccinia*	Loegering and Powers	1962
Hordeum and *Ustilago*	Oort	1963
Caffea and *Hemileia*	Mellow-Sampayo and Noroha-Wagner	1964
Avena and *Ustilago*	Halisky	1965

(After Person, 1966)

The system envisaged by Person (1966) differs in important respects from the system of balanced polymorphism in *H. rostochiensis* as suggested in this thesis. Person's system is essentially dynamic; it depends on a time lag between cause and effect and it collapses if the cause is removed. In an isolated system, if there were no R genes in a population of the host, polymorphism of specificity in a parasite could not be sustained; the V genes would decline to an extremely low frequency maintained by recurrent mutation, which does not come within Ford's definition of polymorphism (page 81).

V genes were certainly not polymorphic in *P. infestans* in Europe when R genes began to be introduced into European potatoes by breeding, because each new R gene retained its effectiveness for years until, presumably, a mutation at the right time and place initiated the resistance-breaking epidemics which eventually

occurred. By contrast, when H genes for resistance to H. rostochiensis began to be introduced into European potatoes, the corresponding specificity genes were certainly polymorphic, despite the fact that the parasite had regenerated in potatoes lacking H genes over a period of more than 100 years. The reason for this has already been suggested; balanced polymorphism of H. rostochiensis is essentially stable under these conditions, because the specificity genes are associated with increased fitness to multiply in fully susceptible potatoes; they are allelic and can show dominance, and are probably maintained in balance by heterozygous advantage, the commonest mechanism promoting balanced polymorphism. It is suggested that this mechanism compensates for the low reproductive rate of H. rostochiensis as compared with P. infestans, and the ensuing immense difference in the rate of which a new pathotype could become established following mutation in these parasites, and is an adaptation to parasitism in the widest sense.

APPENDIX 1.

LIFE HISTORY OF POTATOCYST NEMATODE, HOST RANGE AND WORLD DISTRIBUTION.

APPENDIX 1.

LIFE HISTORY OF POTATO CYST NEMATODE.

The life history of H. rostochiensis Woll. has been studied by Franklin (1951) and later reviewed by Shepherd (1965). In the absence of a potato crop the eggs tend to remain unhatched within the cyst. These encysted eggs represent the persistent or resting stage in the life cycle. In this enclosed condition the eggs have been known to retain their viability for up to 20 to 30 years (Grainger 1958, 1964), although with a progressive decline in hatchability. Hatching is generally greatly stimulated by potato root diffusate. The invasive larvae which emerge from a cyst through the neck or fenestra are in the second stage of development, having already shed their first cuticle, whilst in the egg. They are colourless worms barely visible to the naked eye, sluggish in movement and sexually undifferentiated.

Penetration of the host occurs just behind the growing root tip or where a lateral root emerges. The larva then migrates a short distance through the cortex, leaving a track of disrupted tissue. It finally takes up a position with its head adjacent to the cells of the endodermis and its body lying parallel to the root axis, the tail usually pointing towards the root tip. The cells around the head of the nematode give rise to multinucleate 'giant cells', the contents of which are imbibed through the retractable stylet of the developing larva. There is also a tendency for cells in the region to separate as the middle lamella dissolves. The general effects of these changes are to interfere

with the uptake of water and nutrient salts, with the result that the plants have a sickly appearance and tend to wilt.

Four moults take place within a period of six weeks, after which the sexes are distinct and mature. The female is pyriform, white and opaque, her posterior protruding through a tear in the cortex of the root. The female is sedentary and probably attracts the males by means of chemical attraction. 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 elongated speck on the root to the naked eye. Recent work has shown that fertilisation is essential for egg production (Ellenby 1957; Trudgdill 1967). Multiple matings have been recorded but it is not known for certain if multiple fertilisations can result. The sex of the invasive larvae is determined by environmental conditions and the amount of root space available; those capable of inducing the formation of giant cells in the host become females, while the remainder tend to become males.

The ovaries in the fertilised female develop rapidly, ultimately filling the whole of the swollen body with up to 500 or 600 eggs. In swelling, the body of the female bursts through the root epidermis while the head and neck remain embedded. The females as they first appear are white, and fully ripened cysts and are always some shade of chestnut brown. There may be an intermediate yellow phase, of varying duration and intensity, depending on pathotype. The tough, thickened walls of the brown

cysts are resistant to decay, and so cysts of all ages tend to be more frequent in the parts of a field which were infested first, although the egg population may be higher elsewhere in the field.

HOST RANGE.

Among the European crop plants, potatoes (Solanum tuberosum subsp. tuberosum) and tomatoes (Lycopersicon esculentum) are the only important hosts of potato cyst nematode, while the egg plant (S. melongena L.) is the only other cultivated plant so far recorded as a host (Fassuliotis and Feldmesser, 1954). Some native British plants are included in the list of plants on which cysts have been recorded (Table 5.1.).

Altogether, no fewer than 92 species of the genus Solanum have been recorded as hosts (Ellenby, 1954; Goodey, T., 1956; Goodey, J.B., Franklin and Hooper, 1959; Stelter, 1959), the great majority of them native to South America and Central America.

TABLE 5.1.

List of host plants on which cysts have been recorded.

Host plant	Reference
Solanum dulcamara L.	Franklin (1940)
S. nigrum L.	Franklin (1951) Prummel (1958)
S. miniatum Bernh.	Southey (1965)
S. sarachoides Sendtner.	Bates (1945)
Atropa bella-donna L.	Franklin (1940) Winslow (1954)
Ullucus tuberosus Caldas (Basellaceae)	Bazan de Segura (1953)
Oxalis tuberosa Molina (Oxalidaceae)	Bazan de Segura (1953)
Chenopodium opulifolium Schrad (Chenopodiaceae)	Bazan de Segura (1953)
C. quinoa Willd.	Bazan de Segura (1953)
S. aviculare Forst.	Buhr (1961)

WORLD DISTRIBUTION OF H. ROSTOCHIENSIS.

The potato cyst nematode has been reported in most countries of the world where cultivation of the potato is practised on an intensive scale, as can be seen from the accompanying Table 5.2.

Over half of the records listed since 1950 are first records, but recent discovery does not necessarily indicate recent introduction. The main area known to be affected covers most of temperate Europe and the Mediterranean basin, with probable climatic limits to the north and south, and the range may well be extended eastwards by further discoveries. At present the eastern front of the infestation probably runs through U.S.S.R., through Estonia, Latvia, Lithuania, Byelorussia and part of the Federated Republics in the north, to Israel in the south. The greater part of Asia is still a little known field, so far as plant nematodes are concerned, but interceptions by the U.S. plant quarantine authorities suggest that H. rostochiensis must also occur in Japan.

Bazan de Segura (1952) considers the potato cyst nematode indigenous to the Andes as it has also been recorded in the Andean regions of Bolivia and Argentina (Bell and Segundo Alandia, 1955; Brucher, 1960). Simon (1956) reported that the potato cyst nematode populations infesting the Peruvian highlands were indigenous, while the nematode populations found infesting the coastal plains had arisen as a result of contaminated seed being imported from outside. As regards the spread of the cyst nematode

into adjacent Central America, there are reports of cysts reputed to be identical to those of the potato nematode being found in Mexico (Schick, 1961). However, Campos (1964) found cysts in Mexico resembling those of the potato nematode which must have belonged to a different species, because the larvae failed to invade the roots of potato plants.

TABLE 5.2.

The world distribution of the potato cyst nematode, *Heterodera rostochiensis* Woll.

Country	Reference
Algeria	Anon (1954); Schick (1961)
Argentina	Brucher (1960)
Austria	Anon (1955)
Balearic Islands	Southey (1965)
Belgium	Anon (1958)
Bolivia	Bell and Alandia (1955)
Canada (Newfoundland)	Farstand (1962)
(Vancouver)	Orchard (1965)
Canary Islands	Chamberlain (1961)
Channel Islands	Small (1939); Anon (1958); Anon (1955).
Czechoslovakia	Sedivy and Pohajda (1954)
Denmark	Gram (1955); Mygind (1955); Anon (1958)
Faroe Islands	Southey (1965)
Finland	Anon (1954)
France	Southey (1965)
Germany	Zimmermann (1914)
Great Britain	Morgan (1925); Anon (1954)
Greece	Anon (1954)
Holland	Anon (1954)
Iceland	Anon (1954); Anon (1958)
India	Jones (1961)
Irish Republic	Carroll (1933)
Israel	Anon (1955); Minz (1956)
Italy	Anon (1961)
Lebanon	Anon (1962)
Luxembourg	Anon (1954); Schick (1961)
Mexico	Schick (1961); Southey (1965)
Norway	Anon (1954); Stoen (1956)
Peru	Bazan de Segura (1952)
Poland	Anon (1957); Eis (1964)
Portugal	Anon (1956)
Saar	Anon (1955)
Spain	Anon (1955)
Sweden	Anon (1954); Schick (1961)
Switzerland	Anon (1958)
U.S.A. (Long Island)	Chitwood and Buhrer (1946)
U.S.S.R. (Latvian S.S.R.)	Eglitis and Kaktinya (1959)
(Estonia)	Anon (1957)
(Lithuania)	Anon (1957)
(Ukraine)	Anon (1958)
(Kalirigrad)	Anon (1958)
(Leningrad)	Anon (1958)

APPENDIX 2

THE INHERITANCE OF SPECIFICITY IN RESISTANCE-BREAKING POPULATIONS OF POTATO CYST NEMATODE

APPENDIX 2.

THE INHERITANCE OF SPECIFICITY IN RESISTANCE-BREAKING POPULATIONS OF POTATO CYST NEMATODE.

Introduction.

Pathotype B of potato cyst nematode encysts freely in the roots of potatoes incorporating the resistance-gene H1 ex Solanum tuberosum subsp. andigena, whereas pathotype A virtually fails to encyst in this material, (Dunnett 1957, Howard, 1959). The reverse is true in potatoes incorporating the resistance gene H2 ex S. multidissectum (Dunnett, 1961). These are independently acting genes; together in the same (H1H2) plant, they suppress cyst formation by pathotypes A and B. Therefore, cysts appearing in appreciable numbers on H1H2 plants have to be attributed to a new pathotype, and there is general agreement that this should be called pathotype E.

It has been established, largely through the cooperative officers of the National Agricultural Advisory Service, that pathotype E frequently occurs in English populations, especially in the North.

These facts open up a possibility of investigating the mechanism of inheritance of specificity in potato cyst nematode, bound up with the answers to the following questions. Can pathotype E be produced by genetic recombination between pathotype A and pathotype B? If so, in which generation following mass inter-breeding does pathotype E appear, and in what frequency; if not, what is the reason for the lack of recombination between pathotype A

and pathotype B? This communication sets out to answer these questions.

Materials.

The two base populations of potato cyst nematode, an A-population named "Boghall" and a B-population named "Duddingston", were at least 95% true to type. In order to achieve this, the Duddingston population had been regenerated for the previous seven years in H1 potatoes, a process of selective culture designed to progressively eliminate pathotype A from the population. The original Boghall population contained little or no pathotype B.

The differentially resistant host potatoes, which incorporated either H1 or H2 or both genes, were un-named clones selected from breeding material being assessed commercially. The potato variety Craigs Defiance was used as the fully susceptible host for all populations.

F1 populations were produced by regenerating 1:1 mixtures of the base populations in Craigs Defiance. F2 populations were produced by regenerating F1 populations in Craigs Defiance. An F3 population was produced similarly. These populations are listed under reference numbers in Table 6.1., which records their lines of descent. The last two figures of a reference number indicate the year in which a population originated in egg form.

Methods.

When batches of cysts supplied the inoculum, they were enclosed in small bags or sachets or nylon gauze, which did not

TABLE 6.1. Names and reference numbers of populations multiplied in Craigs Defiance.

P_1	Boghall x Duddingston	Boghall x Duddingston	Boghall x Duddingston
	↓	↓	↓
F_1	160	161	362
	↓	↓	
F_2	261	462	
	↓		
F_3	562		

The last two figures of the reference number refer to the year of egg formation.

restrict the movement of larvae, so that there could be no confusion later between old cysts and cysts of a new generation formed outside the bags. The bags did not contain a counted number of cysts. They contained the complete floats from sub-sample of soil, enough to give an average infectivity of 20 eggs/gm. when the sachet containing a float was buried in a pot containing cyst-free soil. Each float was simply washed into a sachet attached to the stem of a filter funnel by means of a rubber band. The sachets snapped shut when pulled off.

When single cysts were used to supply inoculum, the plants were grown in the special way explained and depicted in Fig.2.1., (page 35).

The main advantage of the method was that the plants grew strongly and uniformly, although crowded together, because they had fairly free root run in good potting soil above, below and between the pots. They had to be pruned at a height of about 1½ feet to prevent lodging. The infected part of the root system was small and restricted, and there could be next to no loss of larvae through the drainage hole because the growing stem blocked it. Only 50-70 gms. of pure sand had to be washed in order to extract all the cysts formed in a pot.

Plants of Craigs Defiance were grown as in Fig. 2.1. when controlled single larva matings were to be attempted. A glass capillary tube was embedded with one end projecting from the sand in each pot. A newly hatched larva was sucked into a hypodermic needle and injected down each tube. About four weeks later up to

TABLE 6.2. Reproduction of populations in series of test potatoes incorporating resistance genes H_1 ex subsp. andigena and H_2 ex S. multidissectum.

Population	Generation	Pathotype	Reproduction		
			H_1 plants	H_2 plants	H_1H_2 plants
Boghall	P	A	-ve	+ve	-ve
Duddingston	P	B	+	-	-
160	F_1	mixed	+	+	-
161	F_1	"	+	+	-
261	F_2	"	+	+	-
362	F_1	"	+	+	-
462	F_2	"	+	+	-
562	F_3	"	+	+	-

six males were also injected down each tube, which meant that they entered the sand in a pot at exactly the same point as had a single larva, which probably increased the chances of mating if the single larva had developed as a female in the interim.

Results.

As indicated in Table 6.2., none of the F populations reproduced in H1H2 plants, although all of them reproduced in H1 plants and H2 plants. From this it could be deduced that they contained no AB recombinants equivalent to pathotype E, but remained mixtures of pathotype A and pathotype B.

The differentially resistant clones and Craigs Defiance were tested against four of the F populations under controlled conditions, using the buried bag technique of inoculation. The yields of cysts were obtained by flotation from the contents of the pot in which each plant had been grown. Six plants of each clone were tested against each population. The mean yields of cysts are recorded in Table 6.3., and are converted to percentages on the theoretical basis that the corresponding yields on Craigs Defiance were the maximum possible for the conditions. Since recombinants were not present, the percentage yields on H2 plants and H1 plants are estimates of the frequencies of pathotypes A and B, respectively. The ratios of pathotype A to B are given in Table 6.4. Pathotype A predominated over pathotype B in the F1 generation, and increasingly so in the succeeding generation.

Since no evidence of interfertility between pathotypes A and B had as yet been obtained, it was necessary to attempt controlled

TABLE 6.3. Relative yields of cysts/gm. air-dried potting soil.

Population	Generation	Yield of cysts/gm.			
		Craigs Defiance	H_1 plants	H_2 plants	H_1H_2 plants
261	F_2	2·85(100%)	0·26 (9·1%)	1·61(56·5%)	negligible
362	F_1	1·95(100%)	0·75(38·5%)	1·40(71·8%)	negligible
462	F_2	3·91(100%)	0·11 (2·8%)	1·20(30·7%)	negligible
562	F_3	2·00(100%)	0·08 (4%)	1·38(69%)	negligible

Initial infestation = 20 eggs/gm.

TABLE 6.4. Ratio pathotype A:B in mixed populations.

Population	Generation	Ratio A:B	
		Observed	Expected if A dominant over B
362	F_1	2:1	3:1
261	F_2	6:1	3:1
462	F_2	11:1	3:1
562	F_3	17:1	3:1

TABLE 6.5. Controlled matings: single larva of one strain + several males of the other.

single larva (♂ or ♀)		♂	No. crosses attempted	No successes	%age success	2nd generation present
Duddingston	x	Duddingston	168	26	15·4	9 cases
Duddingston	x	Boghall	504	72	14·2	13 "
Boghall	x	Duddingston	192	21	11·5	4 "
Boghall	x	Boghall	168	33	19·6	12 "

single larva matings. Over 1000 such matings were attempted (Table 6.5.). Up to 20% of them were successful, and matings between pathotypes were only slightly less successful than within pathotypes. When more than one cyst was recovered as a result of single mating, this was attributed to the uninterrupted production of a second generation. As many as 33 cysts were recovered following the initial mating of a single female.

Discussion.

The results established that pathotypes A and B, as represented by the Boghall and Duddingston populations, respectively, were interfertile; that pathotype A predominated over pathotype B in the F1 generation, in a ratio approaching 3:1; and that repeatedly regenerating mixtures of the Boghall and the Duddingston populations failed to produce AB recombinants.

These facts all point to the conclusion that specificity A is genetically dominant over specificity B in potato cyst nematode. As a working hypothesis, it is suggested that VaVa and Vavb gives specificity A and that vbvb gives specificity B.

As it stands at present, this simple hypothesis precludes the existence of pathotype 0, which is theoretically capable of encysting only on fully susceptible potatoes such as Craigs Defiance and not in H1 or H2 potatoes. It tends to support Howard's conclusion (1967) that pathotype 0 probably does not exist.

Since the ratio of pathotype A to pathotype B was 1:1 in the initial mixed populations, the expected ratio of pathotype A to pathotype B in F1 and succeeding generations was 3:1, assuming

that Hardy-Weinberg equilibrium was established. Table 6.4. shows that the ratio of 2:1 in the F1 generation was near to expectation, but in the succeeding generations the ratio increased rapidly and progressively in favour of pathotype A. Since an essential condition for the establishment of Hardy-Weinberg equilibrium is that there should be no fitness difference between genotypes, it is suggested that pathotype B was less fit than pathotype A. Inherent in this suggestion is the possibility of heterozygous advantage, since in the F1 generation pathotype A was expected to comprise a mixture of heterozygotes and dominant homozygotes in the ratio of 2:1.

This opens up the possibility that pathotypes A and B can coexist in a state of balanced polymorphism in populations of potato cyst nematode, since allelism coupled with heterozygous advantage is the commonest mechanism promoting such a system.

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Note: This is the gist of an unpublished paper presented at the 9th International Nematology Symposium in Warsaw, 1967, by Dr. J.M. Dunnett. The concluding paragraphs dealing with the significance of balanced polymorphism in potato cyst nematode are omitted because this treated the subject less fully than the section of the thesis entitled "Balanced polymorphism in parasitic systems", page 197.

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