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A Synoptic Approach for Crop Loss Assessment Used to Study Wheat. VI* The Pathogen Data and their Relationship to Soil and Cultural Practice Data

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Abstract

As a part of a general investigation of factors that affect wheat crops on Yorke Peninsula, S. Aust., pathogens were measured at 3 and 8 weeks after emergence of the crop and at anthesis.

A first study for regression work showed that, except on the coronal root system at anthesis, the pathogen data were independent of the soil and cultural practice data. Further, it showed that patterning within the pathogens was quite weak and so the value of alternative representations was marginal in this situation.

In a second study, significant relationships were found between logarithmically transformed pathogen data, first within the pathogens between sampling times and root systems, and second between the pathogens and the soil and cultural practice data. The former relationships were mostly of the expected type in that high levels of a particular pathogen tended to persist over sampling times and extend over both root systems. The latter relationships were generally weaker, with the two most marked being (i) a tendency in sandy soils for coronal roots at anthesis to have high levels of *Rhizoctonia solani*, and (ii) for seminal roots at anthesis to have high levels of *Heterodera avenae* when plants were grown in shallow soils on calcareous rocks, particularly where the farmers applied high levels of superphosphate.

Introduction

Pathogens comprise one of several groups of variables that contribute to the observed variation of growth and yield of wheat. In this paper, we consider pathogen measurements taken from 84 sites on Yorke Peninsula, S. Aust., in 1972. The fungi, *Gaeumannomyces graminis* (Sacc.) Arx. and Oliv. var. *tritici* Walker and *Rhizoctonia solani* Kuhn (Anon. 1868; Richardson 1910; Winn 1965), and the nematodes, *Heterodera avenae* Woll. and *Pratylenchus minyus* Sher & Allen, reported as the main pathogens on Yorke Peninsula (Samuel 1928; Johnston 1934; Banyer 1966), were included in the study. Rust fungi, which cause serious crop losses in some years (Webber 1965; Webber and Matz 1970), did not occur in 1972 at the sites considered. Other pathogens reported, including those causing septoria leaf blotch, septoria glume blotch, and powdery mildew, were scarce.

In the first part of this paper, we represent the pathogens in a form appropriate for regression studies aimed at describing variation in the growth and yield of wheat. As in earlier papers of this series, a prime consideration was to minimize correlations among the regressor variables, so not only should the pathogen data be essentially statistically independent within the subset of variables making up the different

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pathogens, but also the pathogen data should not be appreciably correlated with regressor variables in the other subsets that have been referred to in earlier papers.

In the second part of this paper the data are summarized to provide a view of how the pathogens varied in the study area, the patterns of host–parasite relationships, and interrelationships between the pathogens and the soil properties and cultural practices.

Methods and Procedures

Measurements of Pathogens

Fungal pathogens on the separate seminal root and coronal root systems were assessed by measuring lesions on the main root axes. Each root was placed in a shallow Perspex dish and examined with a dissecting microscope. The dish was engraved at intervals of 1 cm, and the numbers of corresponding intervals along each root containing a whole or a portion of a lesion were counted.

The total number of lesion counts on all main seminal root axes and on all main coronal root axes were recorded for three recognizable fungal categories, *G. graminis*, *R. solani* and initially *Pythium* spp. Fungi which could not be readily identified microscopically were grouped as one category, viz. 'other fungi'. *Pythium* spp. were later included in this category because of their low incidence.

For *G. graminis* and *R. solani*, a measured lesion corresponded to the length of vascular tissue showing characteristic blackening and to the length of cortical and vascular necrosis respectively. Diagnostics were the presence of characteristic runner hyphae of *G. graminis* and hyphae typical of *R. solani* associated with cortical breakdown, necrosis and, in advanced cases, the exposure of vascular tissue (Samuel and Garrett 1932). Isolations from lesions on the roots of additional plants collected from the field supported the identifications.

Damage, considered to be caused by insects, was measured when the roots were examined for fungal pathogens and was recognized as distinctive excavations of the cortex which often included underlying vascular tissue. The adjacent tissue showed little disruption and secondary infection was not normally apparent. Insect and fungal damage were rated by the same procedure.

Nematodes were counted after separation from the roots by heating in EDTA at 65°C for 24 h and macerating in an MSE blender at high speed for 20 s (Stynes 1976).

For all analyses presented in this paper each pathogen count was divided by the current dry weight of the plant tops so that the pathogen measurements represented the intensity of infection on the two root systems at the different sampling times.

Foliar pathogens, present only at very low levels in the crops studied, were not measured.

Analytical Approaches

In the initial part of this paper, concerned with presenting the data in a form suitable for regression studies, it was anticipated that low to moderate levels of infection would have little effect on growth and yield, while high levels could have appreciable effect. So it was considered that no transformation of the pathogen data would be appropriate, in spite of the well-known highly positively skewed frequency distributions of such data.

In the second part, aimed at highlighting associations, because of distributional properties, the data were transformed using logarithms, so that significance levels could be estimated by standard procedures. With the untransformed data considered appropriate for the first part, standard procedures could give misleading significance levels.

Attention is drawn to the two approaches used in this study, since each can lead to different results concerning associations between pathogens and between pathogens and the soil and cultural practice data.

Representation of the Pathogen Data for Regression Studies

As shown in earlier papers (Stynes *et al.* 1979; Veitch and Stynes 1981), data can be simplified considerably when appreciable correlations exist within each subset, as well as between various subsets. Consequently, it was appropriate in this instance to examine the interrelationships within the pathogen data as well as between the pathogens and the soil measurements and also between

the pathogens and the cultural practices described previously in Part IV (Stynes and Veitch 1981). The other major subset that could have been considered, comprising the climatic variables, was highly specific to the 1972 season. Climatic factors are highly variable between years, and consequently were not investigated here.

Two procedures were used to simplify the data. Firstly, principal component analyses were used to produce alternative statistically independent variables which could replace the original correlated variables, e.g. Part I (Stynes *et al.* 1979). Secondly, the canonical correlation procedure, which was described in detail in Part III (Veitch and Stynes 1981), was used to examine interrelationships between the relevant subsets. Briefly, this procedure allows for any two subsets of variables to be split into specific variables for the first subset, likewise for the second subset, and common variables, either from the first or from the second subset. Whether common variables are chosen from the first or from the second subset depends on the model being considered. For example, a prediction model relating pathogen data from say, 3 weeks to 8 weeks might use common variables selected from the soil and cultural practice data group rather than the pathogens; in the later stages of growth it would probably be the reverse.

Descriptions of the Pathogen Associations

Patterns of colonization of the roots were studied using the canonical correlation procedure. Initially, relationships between the pathogen measurements taken at 3 weeks and those taken at later samplings were examined. Similarly, relationships between measurements on the seminal roots at 8 weeks and at anthesis, on the coronal roots at 8 weeks and at anthesis, and finally between the seminal and coronal roots at both 8 weeks and anthesis were examined.

The canonical correlation procedure was also used to study the incidence of pathogens in relation to soil properties, cultural practices and cropping histories.

As pointed out earlier, log-transformed pathogen data were used in this series of analyses to permit valid and convenient estimates of significance levels. In instances where the interrelationships between the pathogens were relatively low, it was decided to present the associations in the form of multiple linear regressions.

Results and Discussion

Representation of the Pathogen Data for Regression Studies

Table 1 shows the means, minima and maxima and the standard deviations of all the pathogen data adjusted by top dry weight. Typically minima are zero or very near zero, while the standard deviation nearly always exceeds the mean, the two exceptions being *G. graminis* at anthesis where, on the seminal roots, the two statistics are equal and on the coronal roots the mean of 2·5 is greater than the standard deviation of 1·7. The maximum values were typically about 10 times the mean, ranging from about four times to 50 times. Clearly all data are markedly positively skew.

The following are features of these data.

(a) The very high values at 3 weeks are due to the low top dry weights at this time compared with those at later samplings. This is in contrast to the total numbers, which increased up to anthesis, as might be expected. For example, total *H. avenae* were 33, 71 and 93 at the 3-week, 8-week and anthesis samplings respectively.

(b) In the measurements of the pathogens it will be recalled that the fungi and insects were measured using root lesions while the nematodes were direct counts. Consequently, the means are not directly comparable between the nematodes and the other pathogens, and comparisons have only been made within each group.

(c) Of the nematodes, *P. minyus* was the more frequent pathogen, having a fraction of the total population equal to 0·91 at 3 weeks. At 8 weeks, fractions were equal to 0·88 and 0·92 on the seminal and coronal roots respectively, and at anthesis, fractions were equal to 0·94 on both root systems.

(d) Comparisons of the individual components of *H. avenae*, viz. juveniles, males and females, across the two root systems at the 8-week and anthesis sampling terms are of interest. At 8 weeks, colonization is well established on the seminal roots but not on the coronal roots. On the latter, the colonization that exists is primarily by the juveniles, whereas on the seminal roots there are approximately equal numbers of juveniles, males and females. By anthesis the juveniles are virtually absent and the females are dominant in both root systems, the ratios of males to females being 1 : 5 on the seminal roots and 1 : 3 on the coronal roots.

(e) Among the remaining pathogens (*G. graminis*, *R. solani*, other fungi and insects), *G. graminis* was the most frequent pathogen. *R. solani* followed, at an appreciably lower level (except on the coronal roots at 8 weeks when the order was reversed), then, at still lower levels, were the insects and finally, least of all, were the other fungi.

Initial attempts to simplify the data involved analyses using the principal components procedure. As already noted, the frequency distributions of the adjusted pathogens were markedly positively skew. Consequently, heavy infestations had a disproportionately larger effect on the nature of the alternative principal component representation than did low infestations. This feature seems appropriate in terms of the possible relevance of pathogens to the growth and yield of wheat. However, our data were generally so weakly correlated that these analyses did not produce appreciable simplifications in the data.

Details of the correlations are as follows. At 3 weeks, among the 15 correlations, the largest was 0·31; at 8 weeks on the seminal roots, 8 out of 28 possible correlations exceeded $\pm 0{\cdot}3$, the largest of these being 0·67; at 8 weeks on the coronal roots only 3 out of 28 exceeded $\pm 0{\cdot}3$, the largest being 0·37; at anthesis on the seminal roots 5 out of 28 exceeded $\pm 0{\cdot}3$, the largest being 0·47; and finally on the coronal roots at anthesis 4 out of 28 exceeded $\pm 0{\cdot}3$, the largest of these being 0·45.

Possibly the procedures were useful for the measurements taken at 8 weeks when the first 10 principal components retained on average 91% of the total information, and could replace the 16 original variables. There was a similar retention of information in the first 10 principal components of the analysis of the anthesis data.

Further simplification of the data was attempted using the canonical correlation procedure to examine relationships between the untransformed pathogens and the soil and cultural practices data. Table 2 shows the values of the first canonical correlation coefficient in each of the seven analyses carried out, together with the estimated levels of significance. In all these analyses the principal components of the pathogens, or a subset of them as indicated in the Table, were used, but the evidence for overall relationships was weak. At 3 weeks there were no apparent significant correlations nor were there for the seminal roots at later sampling times. On the coronal roots, the first canonical correlation was 'significant' at both 8 weeks ($P < 0{\cdot}05$) and at anthesis ($P < 0{\cdot}001$) according to the usual tests. However, these tests assume multivariate normality, which is certainly not the case in these data,

Table 1. Simple statistics of pathogens measured on the seminal and coronal roots at successive sampling times, standardized by plant top dry weight (levels of infestation)

Pathogens	Mean	Minimum	Maximum	s.d.
		3 Weeks after Crop Emergence		
Seminal roots				
G. graminis	14·03	0	108·0	23·1
R. solani	9·01	0	85·0	12·4
Other fungi	4·09	0	26·7	5·9
P. minyus	8693·79	0	66625·0	11000·0
H. avenae	846·53	0	5550·0	1160·0
Insects	7·22	0	120·0	17·8
		8 Weeks after Crop Emergence		
Seminal roots				
G. graminis	7·99	0	40·0	9·2
R solani	1·80	0	31·4	4·0
Other fungi	0·18	0	3·3	0·5
P. minyus	1196·16	29·9	11875·0	1887·4
H. avenae (J)[A]	50·53	0	471·4	93·0
H. avenae (M)	42·24	0	484·6	73·7
H. avenae (F)	63·54	0	1400·0	173·2
Insects	0·39	0	8·6	1·4
Coronal roots				
G. graminis	1·53	0	13·3	2·2
R. solani	3·05	0	23·0	3·8
Other fungi	0·07	0	1·0	0·2
P. minyus	109·47	0	724·0	133·5
H. avenae (J)	8·10	0	142·9	20·9
H. avenae (M)	0·72	0	9·7	1·9
H. avenae (F)	1·23	0	12·1	2·8
Insects	0·09	0	1·7	0·3
		Anthesis		
Seminal roots				
G. graminis	1·70	0	11·3	1·7
R. solani	0·11	0	0·8	0·16
Other fungi	0·02	0	0·3	0·05
P. minyus	616·85	3·6	5032·7	951·3
H. avenae (J)	0·28	0	3·9	0·7
H. avenae (M)	5·85	0	53·6	10·5
H. avenae (F)	30·27	0	251·6	51·3
Insects	0·011	0	0·5	0·05
Coronal roots				
G. graminis	2·51	0·25	8·9	1·7
R. solani	0·95	0	5·1	1·2
Other fungi	0·12	0	0·7	0·14
P. minyus	42·62	1·03	303·5	52·9
H. avenae (J)	0·15	0	2·2	0·4
H. avenae (M)	0·65	0	12·2	1·8
H. avenae (F)	2·02	0	24·3	3·5
Insects	0·07	0	0·7	0·1

[A] J, M and F denote juveniles, males and females respectively.

and so the estimates are suspect. In view of these results, and also of the earlier principal component analyses, it was decided to use the pathogen data directly and present the results in regression terms.

Table 2. Estimated first canonical correlations and 'significance' levels from seven canonical correlation analyses between the soil and cultural practice data and principal components of pathogen data subsets corresponding to the separate and combined root systems at each sampling time

Statistics	3 weeks	8 weeks			Anthesis		
	Seminal roots	Seminal roots	Coronal roots	Seminal + coronal roots	Seminal roots	Coronal roots	Seminal + coronal roots
r_1	0·69	0·71	0·70	0·77	0·71	0·82	0·83
P	0·08	0·26	0·03	0·001	0·37	<0·001	<0·001
Number of pathogen principal components included	6	6	8	10	7	5	10

Table 3 summarizes the relevant results. Values of t for non-significant regressors have not been indicated in the Table, but the number of regressors actually used is given by 83 less the number of error degrees of freedom which are shown. The only relationship considered important is that involving *R. solani* on the coronal roots at anthesis where high levels of infestation tended to occur in sandy soils with negative P1 or PS1 values (see Appendix for explanation of symbols). Other relationships are suspect because the lack of homogeneity of variance in the residuals can give unreliable probability estimates from the t values. Significance levels have not been indicated in the Table for this reason.

For the proposed regression study, only the data from the coronal roots at anthesis offer a possibility of reducing the number of variables through common information. However, any omission is of doubtful value.

Descriptions of the Pathogen Associations

In presenting our interpretation of the results for this phase of the study, it must be emphasized that association need not imply causation and that the patterns described here may be specific to this set of data.

As previously mentioned, the pathogen data are highly positively skew in their frequency distributions, with most pathogens having minimum values of zero and having variances increasing with increasing levels of infestation. For this phase of the study, a logarithmic transformation* was reasonably successful in stabilizing the

* If the level of a pathogen infestation is denoted PI, then the transformation was $\ln(PI+\overline{PI}/10)$; the value $\overline{PI}$ was the appropriate arithmetic mean. The additional $\overline{PI}/10$ was needed to avoid infinitely negative logarithms which occur if PI is zero, as is often the case. A new feature arose when the correlations between these variables were inspected, viz. on some occasions these were quite high between the three types of *H. avenae*. Consequently, two alternative variables, $\ln[(PI_J+\overline{PI}_J/10)/(PI_F+\overline{PI}_F/10)]$ and $\ln[(PI_M+\overline{PI}_M/10)/(PI_F+\overline{PI}_F/10)]$ were used instead of $\ln(PI_J+\overline{PI}_J/10)$ and $\ln(PI_M+\overline{PI}_M/10)$. The subscripts J, F and M refer to juveniles, females and males respectively. These new variables relate to the proportions of juveniles to females and males to females. On different root systems and at different sampling times the two new variates and $\ln(PI_F+\overline{PI}_F/10)$ gave far more consistent correlation patterns than did the old. Also the new variables were far less correlated than the old ones.

Table 3. Relationships between the untransformed pathogen data (dependent variables) and measurements of soil properties, cultural practices and cropping histories (regressor variables), expressed in the form of regressions

Values of Student's t on 76, 75 and 77 degrees of freedom for 3 weeks, 8 weeks and anthesis, respectively, are shown

Dependent variables	Regressor variables (soil properties, cultural practices and cropping histories)[A]: PS1	PS2	ln(S8/S3)	CU3	CU4	% Weeds	Depth of seeding	PC2	PC3	% Variation accounted for (Fisher's A)
Pathogens at 3 weeks										
G. graminis							−3·1			15·4
H. avenae								2·2	−3·2	20·0
Pathogens on seminal roots at 8 weeks										
G. graminis	−2·3					3·0				15·6
P. minyus	−4·4									14·7
H. avenae (F)[B]	−3·4		−2·1							12·6
Pathogens on coronal roots at 8 weeks										
G. graminis	−2·1							2·2		14·9
Pathogens on seminal roots at anthesis										
H. avenae (M)		−2·1		−2·6						16·4
Pathogens on coronal roots at anthesis										
R. solani	−4·7	−2·3								26·5
P. minyus					3·3			4·3		20·1
H. avenae (M)					−2·0					13·3
H. avenae (F)		−2·0						3·7		19·6

[A] PS1, PS2 and ln(S8/S3) have been defined in the Appendix. The remaining variables (CU, cultural practices; PC, previous cropping) are a subset of those defined in Part IV (Stynes and Veitch 1981).

[B] M and F denote males and females respectively.

variances after adding one-tenth of the mean value to the untransformed data. This allowed significance levels to be simply estimated for possible relationships between the pathogens and between the pathogens and the soil and cultural practice data.

The transformed data were inspected by individual correlations, by multiple regression procedures and by canonical correlation procedures.

Table 4. Relationships between the transformed pathogen levels at 3 weeks and the levels at later samplings, expressed in the form of regressions

Values of Student's t on 77 degrees of freedom are shown

Dependent variables	Regressor variables (pathogens at 3 weeks): *G. graminis*	Other fungi	*P. minyus*	*H. avenae*	Insects	% Variation accounted for
Pathogens on seminal roots at 8 weeks						
G. graminis	2·8**		2·3*			14·2**
R. solani	−2·2*	3·4*				13·6**
P. minyus			5·8***			28·6***
H. avenae (F)[A]				7·6***		44·5***
Pathogens on coronal roots at 8 weeks						
R. solani			4·0***	−2·8**		17·5**
P. minyus			4·5***			15·7**
Pathogens on seminal roots at anthesis						
P. minyus			5·3***			27·6***
H. avenae				7·7***		41·8***
Insects					4·1***	12·7*
Pathogens on coronal roots at anthesis						
R. solani			5·1***	−2·6*		28·9***
P. minyus	2·1*		6·4***	−2·0*	−2·3*	38·9***
H. avenae (J/F)	−2·0*	2·0*		−2·5*		15·6**
H. avenae (F)				3·3**		13·0**

* $P \leqslant 0{\cdot}05$; ** $P \leqslant 0{\cdot}01$; *** $P \leqslant 0{\cdot}001$.

[A] F and J denote females and juveniles respectively.

The sequence of colonization of the roots by pathogens during the season was examined, and Table 4 shows the relationships between the 3-week data and subsequent samplings. Here and in ensuing Tables, because the regressors are nearly uncorrelated, the squared values of Student's t give fairly accurate indications of the relative contributions of regressors to the model sums of squares. Only those relationships where the percentage of variance associated with the regression is greater than or equal to 12·5 have been included. This represents statistical significance almost at the 1% level, and probably represents a reasonable lower limit of what might be of practical interest. The most marked relationships are of the persistence type where there are positive and highly significant values of t. It is evident that the main pathogens demonstrating persistence are *P. minyus* and *H. avenae*. It is also evident that, where plants had high levels of *P. minyus* at 3 weeks, they were colonized by high levels of *R. solani* later in the season.

In contrast, plants infected by high levels of *H. avenae* at 3 weeks had lower levels of infection by *R. solani* than would normally have been expected. These observations suggest that early colonization of the roots by *P. minyus* encourages infection by *R. solani*, while *H. avenae* has the opposite effect.

Table 5 shows the relationships between the data on the seminal roots measured at 8 weeks and at anthesis. Again, the most marked relationships were of the persistence type and, as may be expected, these were appreciably stronger than those at

3 weeks. Also, colonization by nematodes could have continued to influence subsequent colonization by fungi, in this instance by *G. graminis*. Whereas high levels of *P. minyus* at 8 weeks preceded heavy infection by *G. graminis* at anthesis, *H. avenae* had the opposite effect. Results for the coronal roots (Table 6) were generally similar, although the relationships were appreciably weaker.

Table 5. Relationships between the levels of transformed pathogens on the seminal roots measured 8 weeks after emergence of the crops and those measured at anthesis, presented in the form of regressions

Values of Student's t on 75 degrees of freedom are shown

Dependent variables	Regressor variables (pathogens on seminal roots at 8 weeks): *G. graminis*	*P. minyus*	*H. avenae* (J/F)[A]	*H. avenae* (M/F)	*H. avenae* (F)	% Variation accounted for
Pathogens on seminal roots at anthesis						
G. graminis	4·1***	2·1*	−3·8***			34·5***
P. minyus		10·9***	−2·9**	2·0*		68·9***
H. avenae (J/F)					−3·5***	23·1***
H. avenae (M/F)				5·1***	−2·5*	32·4***
H. avenae (F)			3·0**		16·9***	81·5***

* $P \leqslant 0{\cdot}05$; ** $P \leqslant 0{\cdot}01$; *** $P \leqslant 0{\cdot}001$.
[A] J, F and M represent juveniles, females and males respectively.

Table 6. Relationships between the levels of transformed pathogens on the coronal roots measured 8 weeks after emergence of the crops and those measured at anthesis presented in the form of regressions

Values of Student's t on 75 degrees of freedom are shown

Dependent variables	Regressor variables (pathogens on coronal roots at 8 weeks): *G. graminis*	*R. solani*	*P. minyus*	*H. avenae* (J/F)[A]	*H. avenae* (F)	% Variation accounted for
Pathogens on coronal roots at anthesis						
R. solani	2·4*	4·9***				31·8***
P. minyus			6·7***			42·0***
H. avenae (J/F)					−3·2**	14·9***
H. avenae (F)				3·2**	5·4***	32·1***

* $P \leqslant 0{\cdot}05$; ** $P \leqslant 0{\cdot}01$; *** $P \leqslant 0{\cdot}001$.
[A] J and F represent juveniles and females respectively.

Associations between pathogens on the seminal and coronal roots at 8 weeks (Table 7) were usually confined to strong positive associations within pathogen types; the main exception was the relatively high levels of *R. solani* on the coronal roots of plants that were lightly infected by *H. avenae* and vice versa. At anthesis (Table 8) there were similar associations between fungi and nematodes.

As well as studying the patterns of colonization of wheat roots by the pathogens, their incidence in relation to soil properties, cultural practices and cropping histories were examined. In this study, since the *H. avenae* measures were not being described in terms of their earlier values but in terms of soil properties, cultural practices (CU) and cropping histories (PC) (Stynes and Veitch 1981), near-colinearity due to high correlations will not affect the results from these regression analyses. Consequently, the simpler log-transformed values of the juveniles and males were used instead of the less correlated log ratios used in the previous sections. Table 9 shows the results for the 13 strongest relationships of the 38 investigated.

Generally, low proportions of variation accounted for by the regressions indicate that soil properties and cultural practices did not have a very strong influence on the way in which soil-borne pathogens colonized the roots. The average value of Fisher's A for the six relationships at 3 weeks was 12·9%; at 8 weeks, for the 16 relationships, it was 9·0%; and at anthesis, for the 16 relationships, the average value was 13·0%.

Table 7. Associations between the transformed pathogens on the seminal roots and those on the coronal roots 8 weeks after emergence of the crops, expressed in the form of regressions

Values of Student's t on 75 degrees of freedom are shown

Dependent variables	Regressor variables (pathogens on seminal roots): *G. graminis*	*R. solani*	*P. minyus*	*H. avenae* (J/F)[A]	*H. avenae* (F)	% Variation accounted for
Pathogens on coronal roots						
G. graminis	6·3***					36·7***
R. solani		4·3***		−2·6*	−3·3**	26·5***
P. minyus			3·4***	2·2*		25·4***
H. avenae (F)					4·0***	13·4*

* $P \leqslant 0{\cdot}05$; ** $P \leqslant 0{\cdot}01$; *** $P \leqslant 0{\cdot}001$.
[A] J and F represent juveniles and females respectively.

Table 8. Associations between the transformed pathogens on the seminal roots and those on the coronal roots at anthesis, expressed in the form of regressions

Values of Student's t on 75 degrees of freedom are shown

Dependent variables	Regressor variables (pathogens on seminal roots): *G. graminis*	*R. solani*	*P. minyus*	*H. avenae* (M/F)[A]	*H. avenae* (F)	% Variation accounted for
Pathogens on coronal roots						
G. graminis	4·5***					17·1**
R. solani		2·5*	2·5*		−2·3*	19·0**
P. minyus			7·4***	2·8*		49·1***
H. avenae (J/F)				−2·9**	−4·3***	27·9***
H. avenae (F)				3·8***	5·0***	35·4***

* $P \leqslant 0{\cdot}05$; ** $P \leqslant 0{\cdot}01$; *** $P \leqslant 0{\cdot}001$.
[A] J, F and M represent juveniles, females and males respectively.

Positive values of P1 or PS1 indicate clay soils with high (−0·1 and −15 bar) water contents; positive values of CU2 indicate shallow soils over calcareous rocks; positive values of PC1 indicate high levels of applied nitrogen and of seeding rate; positive values of PC2 identify farmers who cultivated intensively after the first cultivation, including harrowing after seeding; and finally positive values of PC3 identify farmers who cultivated early. The nine coefficients for PS2 had similar relative values to the first nine for P2. So the omission of the linear and quadratic salinity terms meant that positive values for PS2 indicated acid soils. The details in Table 9 show that the highest associations were *R. solani* on the coronal roots at anthesis (32%) and males of *H. avenae* on the seminal roots, also at anthesis (41%). For particular pathogens, the signs of the significant regression coefficients (given by the signs of t in Table 9) were consistent for each root system throughout the season, indicating that a number of definite patterns developed on certain soils where similar cultural practices and cropping histories occurred.

Table 9. Relationships between the transformed pathogen data and measurements of soil properties, cultural practices and cropping histories, expressed in the form of regressions

Values of Student's t on 73 degrees of freedom are shown

Dependent variables	Regressor variables (soil properties, cultural practices, cropping histories): PS1	PS2	CU2	% Medics minus % grasses	% Weeds	Applied phosphorus	Depth of seeding	PC1	PC2	PC3	% Variation accounted for
Pathogens at 3 weeks											
P. minyus		−2·3*					−2·3*		2·1*	−2·5*	27·6***
H. avenae (J)^A								−2·1*		−2·7**	21·8**
Pathogens on seminal roots at 8 weeks											
G. graminis	−2·4*				3·8***						20·1**
P. minyus	−3·2**	−2·3*			2·4*			−2·7**			26·1***
H. avenae (M)			2·0*			2·0*	−2·1*				22·0**
H. avenae (F)						2·1*		−2·2*			17·4**
Pathogens on seminal roots at anthesis											
P. minyus	−2·0*	−2·2*						−3·1**	2·9**		27·0***
H. avenae (M)		−2·1*	3·5***			3·1**	−2·2*				41·0***
H. avenae (F)		−2·0*				2·3*					21·0**
Pathogens on coronal roots at anthesis											
R. solani	−5·1***										31·6***
P. minyus						−2·0*			3·6***		22·9***
H. avenae (M)									2·1*		23·0***
H. avenae (F)			2·1*	2·6*							25·4***

* $P \leqslant 0{\cdot}05$; ** $P \leqslant 0{\cdot}01$; *** $P \leqslant 0{\cdot}001$.

^A J, F and M represent juveniles, females and males respectively.

In general terms, the factors measured appeared to be more strongly associated with the nematodes than with the fungi. Also, at the earliest sampling, previous cropping histories and cultural practices had stronger influences than soil properties *per se*, although the latter increased in importance as the season progressed. This was not surprising since colonization by nematodes is typically most rapid early in the season when soil water is not limiting. Under these conditions the levels of nematode populations and their ability to colonize roots would be strongly influenced by previous cropping histories and cultural practices. Later in the season, as soil water became limiting, the physical soil properties which influenced water availability would be expected to increase in importance.

With regards to successive sampling times, the influences of soil properties and cultural practices on the patterns of colonization were not apparent until the roots were well established and the levels of colonization reasonably high. Hence there was no evidence of these factors influencing colonization of the early developing coronal roots 8 weeks after emergence of the crop.

For specific sampling times, the 3-week data showed that colonization by nematodes was greater when farmers cultivated late than when there were longer periods of bare fallow. Levels of infection by *H. avenae* tended to be lower when farmers used nitrogenous fertilizers and *P. minyus* tended to be more prevalent on shallow-sown crops in alkaline soils.

At week 8 and at anthesis, similar patterns of colonization by nematodes were maintained, with *P. minyus* being more prevalent on alkaline sandy soils and *H. avenae* being more prevalent on shallow soils over calcareous rocks. High numbers of *H. avenae* adults occurred where high levels of superphosphate had been applied to crops, while males were most abundant on shallow-sown crops. With the fungi, *G. graminis* was found to be most prevalent at 8 weeks on the seminal roots of plants growing on sandy soils which, oddly, had a previous history which included a high proportion of weeds. However, this relationship did not persist until anthesis. The strongest single relationship observed was that for *R. solani* at anthesis, which was most prevalent on the coronal roots of plants grown on the sandier soils.

Conclusions

In the first part of this paper, we considered the pathogen data separately and then together with the soil and cultural practice data. The purpose was to select from them a minimum number of variables that are reasonably independent from a statistical viewpoint to use in the later regression studies. In this respect, the pathogens can be considered to be independent of each other and of the soil and cultural practices data. Nevertheless, the option will be kept open to reduce the number of pathogen variables. At 3 weeks there would be no reduction, but at both 8 weeks and anthesis a reduction from 16 to 10 principal components is a possibility.

In the second part of this paper, for general interest, we considered how pathogens varied in the study area, the patterns of host–parasite relationships and inter-relationships between pathogens and the soil properties and cultural practices. Here, the consideration of the data was only of a general nature, and it was convenient to transform the data with logarithms to detect significant associations. This procedure was not appropriate in the first part where pathogen levels adjusted for top dry weight were considered more relevant to crop losses. Some significant, although

weak, associations were evident. Most notably, the patterns of colonization by the pathogens at any one time persisted at successive sampling periods on the same root systems and between root systems of the same plants. This was clearly the strongest pattern of association in these data, and probably the most likely to persist through a different season. This may not be the case with other significant associations detected, which could be highly specific to the particular season of this study. The following associations come into this category. Although pathogens occurred generally throughout the study area, there were higher incidences of *P. minyus* in alkaline soils, of *H. avenae* in shallow soils over calcareous rocks and of *R. solani* in sandier soils. Not surprisingly, the incidence of nematodes was highest when little cultivation was done prior to cropping. More specifically, high levels of *H. avenae* were encountered where high rates of superphosphate had been applied, while the use of nitrogenous fertilizers apparently reduced the level of infection by this nematode.

It is anticipated that surveys would need to be repeated in different seasons to determine whether any patterns recurred consistently. In emphasizing this point it is recalled that in this study foliar pathogens were virtually absent, presumably because of the unusually dry conditions. In other seasons, more favourable for their development, they also would need to be considered.

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Appendix. The variables PS1 and PS2

For analyses relating the pathogen data to the soil and cultural practice data, a problem arose concerning salinity which was measured at each sampling. This meant there were one, two and three measurements at 3 weeks, at 8 weeks and at anthesis respectively. The results given in Part I (Stynes *et al.* 1979) applied only to the last of these situations where the three measures were transformed to mean, linear and quadratic terms. At 8 weeks, a quadratic term was not available, while at 3 weeks neither was a linear term. If S3, S8 and SA denote the salinities at 3 weeks, at 8 weeks and at anthesis respectively, then (1/3)ln(S3.S8.SA) was the mean salinity in Part I. Corresponding means at 8 weeks and at 3 weeks are (1/2)ln(S3.S8) and ln(S3) respectively. Consequently, we were concerned in the present analyses that the coefficients of the rest of the variables defining the principal components could change, depending on the different mean terms and the presence or absence of linear and quadratic terms.

These points were investigated in detail, and it was decided to use the principal components coefficients derived from an analysis omitting the linear and quadratic terms in the log salinities.

Firstly, separate principal component analyses involving each of the mean salinities showed that there were negligible differences in the coefficients defining the principal components, so the different mean terms were not a problem.

Secondly, at 8 weeks the additional variable ln(S8/S3) estimating the linear term was not significantly correlated with any of the soil variables and so was added separately. At anthesis neither the linear term, ln(SA/S3), (Salinity/P of Part I) nor the quadratic term $\ln(S3.SA/S8^2)$, (Salinity/P of Part I) was significantly correlated with any of the other variables, so again they were added separately. The only difference in the new analysis is that the linear and quadratic terms of the log salinities have been removed from the principal components described in Part I, and which were denoted by P1, ..., P6 in Part IV (Stynes and Veitch 1981). We call these new variables PS1, ..., PS6, and they retained 96·7%, on average, of the total information in the nine soil variables remaining after excluding Salinity/M and Salinity/L. Because the coefficients for Salinity/M and Salinity/L were nearly zero in P1, and the other nine coefficients were virtually unchanged between P1 and PS1, PS1 is nearly identical to P1. However, PS2 is different from P2 because the coefficients for Salinity/M and Salinity/L are appreciable in P2. After a scaling adjustment, the remaining nine coefficients are virtually the same in P2 and PS2, so the nature of PS2 can be inferred from Table 3 of Part I.

Similar considerations applied to the means of the pH measurements. There was no need to consider the linear and quadratic terms; see Part I.