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Soil tillage and eyespot: influence of crop residue distribution on disease development and infection cycles

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Abstract

Two deep-working soil tillage tools, one which inverts soil (plough) and one which does not (chisel), were used before sowing wheat after various crop successions combining eyespot host and non-host crops. Soil structure was nearly the same and crop residues were located in the different soil layers. Eyespot sporulation was estimated by visually assessing pot plants which had been on the trial plots for a fixed length of time. Field plants were also assessed for disease at several wheat growth stages. A kinetic equation expressing disease level as a function of degree-days was fitted to the disease levels observed on the field plants. This equation is based on eyespot epidemiology and depends on two parameters reflecting the importance of the primary and the secondary infection cycles respectively. Pot plant and early field plant disease levels and primary infection were closely correlated to the presence of crop residues in the top layer. The amount of residues depended on both crop succession and soil tillage. Where the previous crop was a host crop preceded by a non-host crop, soil inversion buried host residues, thus decreasing the primary infection risk. Where however the previous crop was a non-host crop preceded by a host crop, soil inversion carried the host residues back to soil surface, thus increasing the primary infection risk. Secondary infection was not correlated to either crop succession or soil tillage.

Introduction

In the absence of a suitable host plant, the eyespot pathogen *Pseudocercosporella herpotrichoides* (Fron) Deighton, survives for about 2 to 3 years as a saprophyte on host residues [Macer, 1961a and 1961b; Steinbrenner and Höflich, 1984]. Crop succession is therefore fundamentally important for disease build-up and has been extensively studied in many European countries including France [Huet, 1986], Germany [Steinbrenner and Höflich, 1984], Great-Britain [Prew, 1981; Polley and Thomas, 1991], Denmark [Schulz *et al.*, 1990]. Eyespot is disseminated by spores carried over short distances by wind and rain drops [Glynne, 1953; Fitt and Bainbridge, 1983], and infects the stem base of the host plant. Successful infection requires the presence of infectious crop residues close to soil surface which is influenced by crop succession and soil tillage. The influence of tillage on eyespot has been investigated, but most authors compare ploughing to direct-drilling [Huet, 1986; Brooks and Dawson, 1968] or to no-ploughing without any further specification [Schulz *et al.*, 1990]. Consequences of soil tillage (other than the direct effect on residue distribution) such as effects on soil structure, soil microflora and weed population as well as on wheat growth and development, have not been studied and might indirectly influence disease development. Furthermore if the same plots are either ploughed or direct-drilled for several years, the cumulative effects of these consequences will be even more pronounced. Other authors worked only with one crop succession type [Maenhout, 1975; Mielke, 1983; Grazzeck, 1986] but the influence of residue movement as a consequence of soil tillage is not necessarily the same for different successions.

The consequences of both crop succession and soil tillage on eyespot infection and disease build-up were studied, and more particularly the influence of crop residues in the top soil layer. The study is thus confined to a single consequence of soil tillage, i.e. vertical crop residue movement as influenced by various crop successions.

Materials and methods

Experiments

To compare different vertical movements of crop residues, without any interference from other tillage effects such as soil structure, two deep-working tools were used; one of these inverted soil layers (plough), the other did not (chisel). Soil was tilled in favourable working conditions. Since the consequences of vertical crop residue movement are influenced by the frequency and order of hosts and non-hosts, various successions were chosen:

Location	Chartres (1° 31′ E 48° 28′ N)		Grignon (1° 58′ E 48° 51′ N)		
Succession	A	B	1	2	3
1989–90	**wheat**	**wheat**	alfalfa	alfalfa	alfalfa
1990–91	**wheat**	sunflower	alfalfa	alfalfa	**wheat**
1991–92	rape	**wheat**	alfalfa	**wheat**	**wheat**
	chisel plough	chisel plough	chisel plough	chisel plough	chisel plough
92–93	← Wheat assessed for eyespot →				

Plots were always ploughed before sowing during the three years preceding the test crop. In 1992–93, wheat was sown after either ploughing or chiselling. At Chartres, each 'crop succession x soil tillage' combination was replicated four times, whilst at Grignon only two replicates were used. Plot area was 17 m × 5.25 m at Grignon and 6 m × 12 m at Chartres. After chiselling or ploughing, all plots at a given location were harrowed and sown on the same day (15th October at Grignon, 16th at Chartres), at the same density (400 grains m^{-2} at Chartres, 300 at Grignon). The cultivars sown were eyespot susceptible: Soissons at Chartres, Fidel at Grignon. No foot disease fungicide was applied. The same herbicides, insecticides and ear and leaf disease fungicides were used on all plots. At Chartres, soil nitrogen residues were measured at winter end to determine the nitrogen fertilizer requirements (177 U after rape, 147 U after wheat). At Grignon, every plot received 120 U. At both locations, nitrogen was applied twice, the first during tillering and the second at Zadoks 30 [Zadoks *et al.*, 1974].

Samplings and measurements

Soil profile. For each 'crop succession x soil tillage' combination, the soil profile was described in early spring to determine the depth and structure of the various layers resulting from soil tillage, according to the description method of Hénin *et al.* [1969] as improved by Gautronneau and Manichon [1987]. For each layer and for each kind of crop residue, 3 classes were distinguished: absence, scarce presence and general presence.

Wheat growth and development. Plants m^{-2} were counted at plant emergence and then monitored, together with tillering, at those growth stages at which field plants were assessed for eyespot.

Quantification of winter sporulation. On each plot, 3 series of 5 pots, each containing 10 wheat plants at 1-leaf-stage, were left for a period corresponding to a fixed sum of degree days (Table 1). The wheat cultivars used were the same as those in the field. After a given period, each of the 3 series was transferred into the greenhouse where they were left for incubation. To accommodate slow and fast growing pathogen types, the pots were left for at least 400 degree-days in the greenhouse before visual assessment for eyespot. For every plot, a mean percentage of diseased plants was thus calculated for each of the 3 series.

The proportion of plants infected during each period depends on the amount of inoculum available and the occurrence of conditions favourable for sporulation, dispersal and infection. Experimental treatments were compared, but not sampling periods and sites.

Disease assessment on field plants. Field plants were assessed for eyespot at 4 wheat growth stages (Zadoks 15, 30, 50 and 80). For each stage and plot, a fixed number of plants (30 at Chartres, 50 at Grignon) were sampled and visually assessed for eyespot. Results are expressed as percentages of diseased plants.

At growth stage 80, the *P. herpotrichoides* varieties responsible for disease symptoms were identified *in vitro*. Diseased tillers were superficially disinfested to destroy saprophytes, then transferred to Potato-Dextrose-Agar. After a 10-day-incubation at 20° C, form, size and colour of the colonies were used to distinguish *P. herpotrichoides* var. *herpotrichoides* from var. *acuformis* [Nirenberg, 1981].

Table 1. Length of stay on field for pot plants

A. Chartres				B. Grignon			
Series	Length of stay		Cumulative degree-days	Series	Length of stay		Cumulative degree-days
	From	To			From	To	
1	2-11-92	8-12-92	286	1	2-11-92	7-12-92	297
2	8-12-92	29-1-93	288	2	7-12-92	3-2-93	324
3	29-1-93	6-4-93	300	3	3-2-93	2-4-93	307

Cumulative degree – days were calculated with basis = 0 °C.

Data analysis

Linear model. For spore quantification, an analysis of variance was performed on eyespot frequency with series, crop succession and soil tillage as factors:

*%plants with eyespot = constant + series effect + crop succession effect + soil tillage effect + interaction crop succession*soil tillage* (1)

For disease on field plants, an analysis of covariance was performed for each assessment stage with the same factors as in model (1) and with two wheat growth and development indicators as covariables:

*%plants with eyespot = constant + block effect + crop succession effect + soil tillage effect + interaction crop succession*soil tillage + a·plant number per m^2 + b·tiller number per plant* (2)

At growth stages 50 and 80, the percentage of tillers blackened by take-all (*Gaeumannomyces graminis* var. *tritici*) was added as a covariable to model (2) because this blackening could have concealed eyespot symptoms. The final models contained only those factors and/or covariables for which the probability values of the statistical zero hypothesis test were lower than 5%. If these values were higher than 5%, the contribution due to the factor or covariable was considered not significant. These analyses were performed with the General Linear Model (GLM procedure) of the SAS software (Statistical Analysis System, SAS Institute Inc, 1989). The sum of squares used to calculate the probability values for each factor or covariable, was adjusted to all terms present in the model and did thus not depend on their order of appearance in the model (type III sum of squares of the GLM procedure).

Disease build-up as a function of thermal time. There are two possible sources of eyespot inoculum: (a) host residues close to soil surface [Macer, 1961a, 1961b; Steinbrenner and Höflich, 1984] that give rise to conidia in the form of primary inoculum (p) which we will suppose to be constant for the given year; (b) secondary inoculum, i.e. conidia from developing lesions on living plants [Rapilly *et al.*, 1979; Moreau *et al.*, 1990]. All plants with visible eyespot (i) were considered as being potential producers of secondary inoculum. To each inoculum type is associated an infection rate: k_1 associated to the primary infection cycle based on infectious crop residues, and k_2 associated to the secondary infection cycle based on infectious lesions on living plants. These rates are presumed not to vary with time. If i is the number of diseased plants, then $n - i$ is the number of healthy plants with n being the total number of plants. Disease evolution speed, i.e. the variation of diseased plants per degree-day, may be expressed as a differential equation where k_1, k_2 and p are constants, according to similar equations built by Van der Plank [1963] for airborne pathogens:

$$di/dt = (k_1 \cdot p + k_2 \cdot i) \cdot (n - i) \qquad (3)$$

To model the percentage of diseased plants (y), equation (3) was divided by n as n does not depend on time (no plant loss during winter or due to diseases etc.) If furthermore we define $c_1 = k_1 \cdot p$ associated to the primary cycle and $c_2 = k_2 \cdot n$ associated to the secondary cycle, then:

$$dy/dt = (c_1 + c_2 \cdot y) \cdot (1 - y) \qquad (4)$$

c_1 and c_2 do not depend on time. After integration, we get the following equation, where time t is expressed as cumulative degree-days (basis 0 °C) since sowing:

$$y = \frac{1 - \exp(-(c_1 + c_2)t)}{1 + c_2/c_1 \exp(-(c_1 + c_2)t)} + \text{constant} \qquad (5)$$

As we know that at sowing ($t=0$), there are no diseased plants and that therefore $y=0$, the constant is also O. The kinetic equation expressing disease level as a function of time and of a pair of parameters depending on field location and environment (climate, soil, ...) as well as cropping system, thus becomes:

$$y = \frac{1 - \exp(-(c_1 + c_2)t)}{1 + c_2/c_1 \exp(-(c_1 + c_2)t)} \qquad (6)$$

Disease level was only assessed at 4 stages on our field trials which was insufficient to judge the adequacy of the chosen equation. Therefore, the kinetic equation was first tested on a plot assessed every two weeks after growth stage 30. This plot was chosen at Le Rheu (1°43′ W, 48°04′ N), a location usually favourable to eyespot [Rapilly *et al.*, 1979]. Wheat was sown the 16th October at 225 grains m^{-2}; neither nitrogen fertilizer or foot disease fungicides were applied.

After this preliminary test, equation (6) was adjusted to eyespot build-up on the different plots of a given 'crop succession x soil tillage' combination. We used the Non-Linear Model (NLIN) procedure of SAS based on minimisation of square sums weighted by the inverse of the variance corresponding to each assessment stage. After a series of iterations, this adjustment estimated the parameters c_1 and c_2 for each experimental treatment.

Construction of a model classifying cropping systems according to their eyespot risk. On each of the two groups of parameter values, we tested a linear model (analysis of variance) explaining parameter value as a function of field location, crop succession and soil tillage. The initial model was as follows:

$$parameter = constant + location\ effect + crop\ succession\ effect + soil\ tillage\ effect + interaction\ crop\ succession{*}soil\ tillage \qquad (7)$$

As before, the final model only contains those factors for which the probability values of the statistical zero hypothesis test were lower than 5%. If the condition of variance homogeneity necessary to apply a linear model is not fulfilled, the Box and Cox [Box *et al.*, 1978] transformation was used to homogenize variance: if the linear regression $ln(variance(parameter)) = a + b \cdot ln(parameter)$ was significant, the parameter c_i was transformed as follows:

$$c^{transformed} = c^{1-b/2}$$

Results

Soil profile description

Grignon. The first layer (Table 2), i.e. the seed bed prepared for wheat, was mostly composed of fine earth. In all plots, depth varied between 8 and 10 cm and it always contained wheat straws in succession 3 regardless of soil tillage and in succession 2 if the plots were chiselled, otherwise alfalfa residues. For succession 1, this layer always contained alfalfa residues, sometimes mixed with gramineae residues. The second layer, beneath the seed bed, was 19 to 25 cm deep, depending on experimental treatment. It had a massive structure resulting from the coalescence of the clods formed by soil tillage. In all plots, a high porosity was visually discernible and this layer did not hinder root development. On chiselled plots, this layer contained aerial alfalfa residues in case of successions 1 and 2, otherwise wheat straws. On ploughed plots, alfalfa residues occurred in the case of succession 1, and otherwise wheat residues. The third observed layer, usually about 10 cm thick, was not disturbed when soil was tilled for wheat sowing. It was of massive structure, but fissures due to the alternation of humidification-desiccation in the loamy clay soil, made root passage possible. In all plots, it contained undisturbed alfalfa tap roots which were more or less decomposed depending on when the last alfalfa crop was grown.

Chartres. Where the plot was ploughed, the soil structure of the first layer was finer. The second and third layers had a porous structure favourable to root growth similar to the structure of the second layer at Grignon. On chiselled plots, the seed bed contained residues of the previous crops: rape residues in succession A and wheat straws in succession B. On ploughed plots, it contained wheat straws in succession A, sunflower stems and a few wheat straws in succession B. The second layer of chiselled plots mostly contained residues from the 1990–91 crops: wheat straws in succession A and sunflower stems in B. Where however the plots were ploughed, the second layer contained residues from both previous and 1990–91 crops. The third layer not having been disturbed by either plough or chisel, contained wheat straws, probably left from the 89–90 wheat crop.

Wheat growth and development

At Grignon, neither soil tillage nor crop succession had any influence on density, plant emergence or tiller-

Table 2. Residue position according to crop succession and soil tillage

A. Grignon							
Succession		1		2		3	
89–90		alfalfa		alfalfa		alfalfa	
90–91		alfalfa		alfalfa		**wheat**	
91–92		alfalfa		**wheat**		**wheat**	
	Soil tillage	chisel	plough	chisel	plough	chisel	plough
Horizon	depth			Residue position			
1 Seed bed	8 to 10 cm	alfalfa (gramineae)	alfalfa (gramineae)	wheat	alfalfa	wheat	wheat
2 Tilled by chisel or plough	19 to 25 cm	alfalfa	alfalfa	alfalfa	wheat	wheat	wheat
3 Not disturbed by chisel nor plough	29 to 33 cm	alfalfa	alfalfa	alfalfa	alfalfa	alfalfa	alfalfa

B. Chartres					
Succession		A		B	
89–90		**wheat**		**wheat**	
90–91		**wheat**		sunflower	
91–92		rape		**wheat**	
	Soil tillage	chisel	plough	chisel	plough
Horizon	depth				
1 Seed bed	4 to 7 cm	rape	wheat	wheat	sunflower (wheat)
2 Tilled by chisel or plough	14 to 24 cm	wheat	rape (wheat)	sunflower	wheat (sunflower)
3 Not disturbed by chisel nor plough	27 to 30 cm	wheat	wheat	wheat	wheat

Residues indicated between brackets are only rarely found.

Table 3. Influence of vertical crop residue movement on eyespot sporulation (% of diseased pot plants exposed to inoculum on field plots)

Site	Chartres	Grignon
r^2 (1)	0.76	0.92
Significance of effects		
Series	0.0001	0.0001
Succession	0.0001	0.0008
Soil tillage	0.0034	0.0469
Succession*tillage	0.0001	ns
Block		0.0059

(1) The percentage of variance accounted for by the model. The tested model was: % of diseased pot plants = constant + series effect + crop succession effect + soil tillage effect + interaction crop succession*soil tillage + block effect (only at Grignon).

ing. At Chartres, tillering varied however slightly with soil tillage (2.73 tillers plants^{-1} at growth stage 80 on chiselled plots, 2.47 on ploughed plots). Plant emergence and density were not affected. None of the wheat growth and development covariables was related to eyespot level at any stage assessed.

Quantification of winter sporulation

At both locations, infection and sporulation depended on series, crop succession and soil tillage (Table 3). Crop succession was more significant than soil tillage. Both at Chartres and at Grignon (Table 4), pot plants were most diseased when the previous crop was wheat (successions 2, 3 and B). This phenomenon was even more pronounced if two wheat crops preceded the assessed crop (succession 3 at Grignon). However sporulation occurred on the plots of succession 1 where no wheat had been grown for three years. Where the previous crop was wheat (succession 2, 3 and B), sporulation was higher after chiselling than after ploughing. Where the previous crop was not wheat but itself preceded by wheat (succession A at Chartres), ploughing vs. chiselling increased sporulation. Where the previous crop was alfalfa (succession 1 at Grignon), sporulation was also higher after chiselling.

Table 4. Eyespot infections estimated by pot plant assessment (% of diseased pot plants exposed to inoculum on field plots)

A. Chartres							
Series		November		December–January		February–March	
Soil tillage		chisel	plough	chisel	plough	chisel	plough
Crop succession							
Wheat/rape	(A)	17	25	18	32	4	12
Sunflower/wheat	(B)	69	47	79	34	40	8
Mean		40		41		16	
B. Grignon							
Series		November		December–January		February–March	
Soil tillage		chisel	plough	chisel	plough	chisel	plough
Crop succession							
Alfalfa/alfalfa	(1)	78	54	8	5	0	0
Alfalfa/wheat	(2)	94	84	39	15	0	0
Wheat/wheat	(3)	92	84	51	43	0	0
Mean		81		27		0	

Table 5. Influence of vertical crop residue movement on disease level (% of diseased field plants)

A. Chartres				
Stage	15	30	50	80
$r^{2(1)}$	0.75	0.37	0.69	0.74
Significance of effects				
Succession	0.0006	0.0127	0.0020	0.0001
Soil tillage	0.0325	ns	0.3019(2)	ns
Succession*tillage	0.0157	ns	0.0082	ns
B. Grignon				
Stage	15	30	50	80
$r^{2(1)}$	0	0.63	0.91	0
Significance of effects				
Succession	ns	0.0704(3)	0.0140	ns
Soil tillage	ns	0.0421	0.0297	ns
Succession*tillage	ns	ns	0.0218	ns
%Blackened tillers			0.0309	ns

(1) The percentage of explained variability r^2 was calculated for a model composed only of significant effects at alpha = 5%.
(2) Although the probability value associated to this factor is higher than the chosen threshold, it is included in the final model as its interaction with another factor is significant.
(3) Although the probability value associated to this factor is higher than the chosen threshold, it is included in the final model because otherwise no significant model would have been possible.
ns = The effect is not significant at alpha = 5%.
The tested model was: % of diseased plants = constant + crop succession effect + soil tillage effect + interaction crop succession*soil tillage + a·plants m^{-2} + b·tillers $plant^{-1}$ + c·% of tillers blackened by take-all (only at stages 50 and 80) + block effect (only at Grignon).

Table 6. Eyespot assessment on field plants (% of diseased field plants)

A. Chartres									
Zadoks stage		15		30		50		80	
Soil tillage		chisel	plough	chisel	plough	chisel	plough	chisel	plough
Succession									
Wheat/rape	(A)	5	7	10	4	8	41	76	71
Sunflower/wheat	(B)	32	13	20	17	64	47	92	93
Mean		14		13		40		83	
B. Grignon									
Zadoks stage		15		30		50		80	
Soil tillage		chisel	plough	chisel	plough	chisel	plough	chisel	plough
Succession									
Alfalfa/alfalfa	(1)	20	19	14	6	38	16	47	26
Alfalfa/wheat	(2)	18	7	42	10	48	34	67	39
Wheat/wheat	(3)	11	6	36	27	41	52	49	58
Mean		13		23		38		48	

Assessment of eyespot on field plants

Neither *plant number* m^{-2} nor *tiller number plant*$^{-1}$ covariables were significant at any location (Table 5). At Chartres, crop succession was always significant and disease level was higher for succession B than for succession A (Table 6). Soil tillage effect was only significant for growth stages 15 and 50 and then less than crop succession. Ploughing increased eyespot infection after succession A and decreased it after succession B (Table 6). At Grignon, no significant effect was found for growth stages 15 and 80. For the other two stages, both crop succession and soil tillage effects were significant (Table 5). Disease level was highest for successions 2 and 3 and lowest but not zero for succession 1 (Table 6). At growth stages 30 and 50, chiselling vs. ploughing increased eyespot infection. At stage 80, there was a negative correlation between the eyespot level and the percentage of tillers blackened by take-all. *In vitro* identification showed that at Grignon, all symptoms were due to *P.h.* var. *herpotrichoides*. At Chartres, the proportion of the different varieties partly depended on crop succession: succession A gave a higher proportion of *P.h.* var. *acuformis* (4% of eyespot lesions) and a lower percentage of var. *herpotrichoides* (97%) whereas for succession B only var. *herpotrichoides* was found.

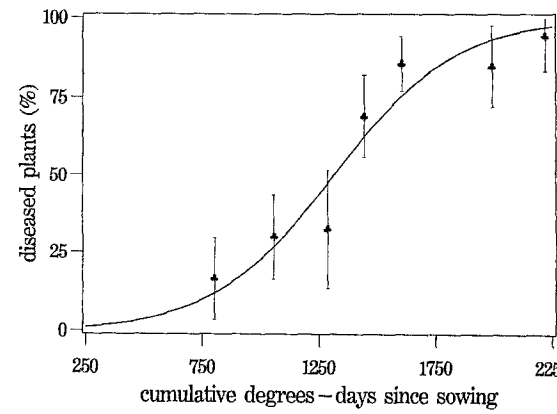

Fig. 1. Test of the kinetic equation: eyespot evolution as a function of cumulative degree-days since sowing (simulated values —; observed values ♣).

Disease development as a function of 'cumulative degree-days'

The test of the kinetic equation on the frequently assessed plot (Fig. 1) shows that the chosen equation is well adapted to describe general eyespot evolution. The adjustment quality is high (Table 7). At Chartres and Grignon, the adjustment quality of the kinetic equation (6) to assessment data was also good (mean $r^2 = 0.97$ at Chartres, mean $r^2 = 0.94$ at Grignon). Simulated curves did however not take into account minor variations as the disease decrease between growth stages 15 and 30 (Table 6).

Table 7. Non-linear least squares summary statistics for the test of the kinetic equation

	Degrees of freedom	Summ of squares
Source		
Model	2	2.99
Error	5	0.05
Uncorrected total	7	3.04
Corrected total	6	0.61

Table 8. Linear model for parameters c_1 and c_2 associated to primary and secondary eyespot infection cycles

Parameter	c_1	c_2
r^2 (1)	0.99	0.51
Significance of effects		
Site	ns	0.0202
Crop succession	0.0062	ns
Soil tillage	0.2543(2)	ns
Succession*tillage	0.0126	ns

(1) The percentage of explained variability r^2 was calculated for a model composed only of significant effects at alpha = 5%.
(2) Although the probability value associated to this factor is higher than the chosen threshold, it is included in the final model as its interaction with another factor is significant.
ns = the effect is not significant at alpha = 5%.
The tested model was: parameter^t = constant + site effect + crop succession effect + soil tillage effect + interaction crop succession*soil tillage where $t = 1 - 1.848/2$ (Box and Cox [Box *et al.*, 1978] transformation using ln (variance) = constant + 1.848 ln (c_1)).

Linear models for equation parameters associated to primary and secondary infection cycles

Succession B at Chartres and succession 2 at Grignon are considered as being of similar type. Only four successions are distinguished in the following models: alfalfa/alfalfa (succession 1 at Grignon), wheat/non-wheat (succession A at Chartres), non-wheat/wheat (succession 2 at Grignon and succession B at Chartres), wheat/wheat (succession 3 at Grignon).

Parameter c_1 associated to primary infection cycle. All factors of the initial model (7), except location effect, were statistically significant (Table 8). Crop succession was more significant than soil tillage. Parameter values were higher where the previous crop was wheat (successions 2/B and 3), but a second wheat in the succession (succession 3) did not further increase the values (Table 9). Succession 1 had a lower c_1 value than succession 2 and 3 but it was not zero. If the previous crop was wheat or alfalfa, chiselling increased the parameter value whereas it decreased it in succession A (the previous crop being rape).

Parameter c_2 associated to secondary cycle. The only significant effect was the location effect (Table 8) with a higher c_2 value at Chartres than at Grignon (Table 9). The variability explained by this model was low ($r^2 = 0.51$) compared to that associated to the c_1 linear model ($r^2 = 0.99$).

Discussion

Soil profile description showed that in all plots, the top soil layer (which contains the infectious residues) was mostly composed of fine earth. Clods were slightly more frequent on chiselled plots, but this difference should not have influenced eyespot sporulation. Furthermore it did not affect plant density. The depth of the underlying layers varied slightly, but their structure had little effect on root and shoot development or tillering. We may therefore consider soil structure as similar whatever the tillage or the crop succession. Soil profile description confirms that the position of crop residues depended both on soil tillage and crop succession. If the previous crop was a possible host, either wheat [Steinbrenner and Obenauf, 1988] or Gramineae such as rye-grass *Lolium perenne* [Ponchet, 1959; Maenhout, 1975] which were frequently found on alfalfa plots, then chiselling allowed host residues to accumulate in the top layer whereas ploughing buried these same residues into the deeper layers. If, on the other hand, the previous crop was a non-host crop and the crop preceding this again a host crop, then ploughing carried host residues back to the top layer whereas after chiselling, the top layer contained no host residues.

According to pot plant assessment, successful autumn and winter infections, and therefore spore production, were highest on those plots where the amount of host residues was largest in the top layer, i.e. if the previous crop was wheat and if the plots were chiselled. Ploughing decreased both wheat residue quantity in this top layer and pot plant infection. These results are consistent with those of Mielke [1983] who further-

Table 9. Values for parameters c_1 and c_2 associated to primary and secondary eyespot infection cycles (Mean ± standard-error)

A. Parameter c_1					
Site		Chartres		Grignon	
Soil tillage		chisel	plough	chisel	plough
Crop succession					
Alfalfa/alfalfa	(1)			$1.34 \cdot 10^{-4} \pm 6.28 \cdot 10^{-5}$	$4.23 \cdot 10^{-5} \pm 1.41 \cdot 10^{-5}$
Wheat/non-wheat	(A)	$4.64 \cdot 10^{-8} \pm 4.10 \cdot 10^{-8}$	$1.13 \cdot 10^{-5} \pm 5.51 \cdot 10^{-6}$		
Non-wheat/wheat	(2, B)	$1.93 \cdot 10^{-4} \pm 6.25 \cdot 10^{-5}$	$3.25 \cdot 10^{-5} \pm 1.80 \cdot 10^{-5}$	$1.94 \cdot 10^{-4} \pm 1.37 \cdot 10^{-4}$	$7.37 \cdot 10^{-5} \pm 2.72 \cdot 10^{-5}$
Wheat/wheat	(3)			$3.59 \cdot 10^{-4} \pm 1.65 \cdot 10^{-4}$	$3.61 \cdot 10^{-5} \pm 2.55 \cdot 10^{-5}$
B. Parameter c_2					
Site		Chartres		Grignon	
Soil tillage		chisel	plough	chisel	plough
Crop succession					
Alfalfa/alfalfa	(1)			$1.08 \cdot 10^{-3} \pm 5.30 \cdot 10^{-4}$	$1.11 \cdot 10^{-3} \pm 3.31 \cdot 10^{-4}$
Wheat/non-wheat	(A)	$6.63 \cdot 10^{-3} \pm 5.32 \cdot 10^{-4}$	$3.38 \cdot 10^{-3} \pm 3.62 \cdot 10^{-4}$		
Non-wheat/wheat	(2, B)	$2.09 \cdot 10^{-3} \pm 5.30 \cdot 10^{-4}$	$3.63 \cdot 10^{-3} \pm 4.17 \cdot 10^{-4}$	$2.23 \cdot 10^{-3} \pm 1.26 \cdot 10^{-3}$	$1.15 \cdot 10^{-3} \pm 3.68 \cdot 10^{-4}$
Wheat/wheat	(3)			$0 \pm 7.60 \cdot 10^{-4}$	$2.54 \cdot 10^{-3} \pm 8.20 \cdot 10^{-4}$

more measured eyespot infectivity of the top layer by growing wheat on soil sampled from this layer and showed that eyespot infectivity is higher after chiselling than after ploughing. The same was true where the previous crop was alfalfa with Gramineae, although pot plant infection was lower as Gramineae residues produce less eyespot inoculum than wheat. Where the assessed pot plants had been on plots with a non-host as a previous crop and a host as the crop preceding that again, then both host residue quantity in the top layer and pot plant infection were reduced by chiselling vs. ploughing. In both cases, spores arising from these host residues were considerably less than those from host residues left from the immediate previous crop, as the amount of the inoculum source decreases with time [Steinbrenner and Höflich, 1984].

Field plant infection depended closely both on crop succession and soil tillage until growth stage 50 as did pot plant infection. The infection levels which we observed on the wheat/rape/wheat agreed with the findings of Maenhout [1975] for a wheat/potato/wheat succession and Grazzeck [1986] for a wheat/pea/wheat succession. However our eyespot assessments for wheat/wheat successions were not consistent with previous report [Brooks and Dawson, 1968; Huet, 1986]. Even Mielke [1983] observed more eyespot after ploughing despite his results on eyespot sporulation and top layer infectivity. However in his trial, plant emergence was lower after chiselling and low plant density is known to decrease eyespot risk considerably [Glynne, 1951; Huet, 1986; Groll and Luzi, 1991]. In our trials however, the effects of crop residue distribution were not masked by plant density which varied little and was not correlated to eyespot level. We have thus been able to correlate soil inversion, host residue location, spore production and early field plant infection.

Until heading, field plant infections seem to depend on the amount of infectious crop residues in the top layer. These results are consistent with those of Cox and Cock [1962] who related field plant infections to the number of wheat straws on the soil surface for various crop successions without any reference to soil tillage. But as in these trials, their late disease assessment did not show any relation to infectious residues.

This study shows the value of a kinetic approach using epidemiological knowledge to study the relationship between cropping systems and infection cycles. It was feasible to build a simple but robust equation based on two parameters related to the primary and secondary infection cycles. The kinetic equation correctly simulated global eyespot evolution and clearly showed the differences between cropping systems. It did not however represent microvariations which was not the initial aim.

The analysis of the linear models explaining parameter values associated to evolution curves confirms the existence of several mechanisms, the first dominating

at the beginning of eyespot infection and the other at the end. Parameter c_1 associated to the primary cycle was always highest when top layer host crop residue quantity was highest, just as autumn and winter spore production. The secondary cycle in contrast, did not depend on either crop succession or soil tillage, but only on location. The difference might be due to environmental conditions, to wheat cultivars or to the pathogen population: *P.h.* var. *acuformis* was only present on succession A in Chartres which had a larger secondary cycle; at this site, plant density was also higher and tillering lower than at Grignon. No previous work exists which might help explain this observation.

Soil inversion as a result of plough use was shown to be of major importance for eyespot control (even if crop succession was the dominant effect): its efficiency is reducing eyespot levels depends upon whether the previous crop and/or the crop preceding that again are host crops. It probably also depends on the inversion angle while ploughing which may vary considerably: in these trials, complete layer inversion was intended and obtained as verified by the soil profile analysis. These various elements help to explain why, according to literature, ploughing results in such variable effects on disease; they also help to define more precisely the agronomical basis for choosing soil tillage modes according to crop succession.

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