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Effects of stem canker (*Leptosphaeria maculans*) and light leaf spot (*Pyrenopeziza brassicae*) on yield of winter oilseed rape (*Brassica napus*) in southern England

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The relationships between yield loss and incidence or severity of stem canker and light leaf spot in winter oilseed rape were analysed by correlation and regression analyses, using data from experiments at Rothamsted, England in 1992/93, 1994/95 and 1995/96. Growth stages (GS) 6,3/6,4 and 4,0/4,5 were identified as the critical points for relating percentage yield loss to stem canker and light leaf spot (on stems), respectively. Critical point (CP) and area under disease progress curve (AUDPC) models relating percentage yield loss to combined incidence or severity of stem canker and light leaf spot (stems) in each experiment were constructed by linear regression. There were no differences in the CP models for incidence between 1992/93, 1994/95 and 1995/96 experiments, or in the AUDPC models for incidence between 1992/93 and 1994/95 experiments. Therefore, a general CP model relating percentage yield loss (ΔY) to combined incidence of stem canker (S_i) at GS 6,3/6,4 and light leaf spot (stems) (L_i) at GS 4,0/4,5 was constructed using data from the three experiments: $\Delta Y = 0{\cdot}85 + 0{\cdot}079S_i + 0{\cdot}065L_i$ ($R^2 = 43{\cdot}7\%$, $P < 0{\cdot}001$, 92 df). A general AUDPC model relating ΔY to the AUDPC of combined incidence of stem canker (S_{ia}) from GS 5·7 to GS 6·5 and light leaf spot (stems) (L_{ia}) from GS 4·0 to GS 6·3 was constructed using data from the 1992/93 and 1994/95 experiments: $\Delta Y = 0{\cdot}07 + 0{\cdot}00096S_{ia} + 0{\cdot}0026L_{ia}$ ($R^2 = 43{\cdot}6\%$, $P < 0{\cdot}001$, 68 df). These two general yield-loss models were tested with data from Rothamsted in 1993/94 and Boxworth in 1992/93. The predictive accuracy of the CP model based on combined incidence of stem canker and light leaf spot (stems) was better than that of the AUDPC model. Yield losses predicted by summing the estimates from individual models for incidence of stem canker alone (GS 6,3/6,4) and light leaf spot alone (on leaves at GS 3,3) were greater than observed yield losses in experiments at Rothamsted in 1992/93, 1993/94, 1994/95 and 1995/96 and at Boxworth in 1992/93.

Keywords: combined yield loss, *Leptosphaeria maculans*, light leaf spot, *Pyrenopeziza brassicae*, stem canker, winter oilseed rape

Introduction

Most work on crop yield loss due to disease has concentrated on effects of individual diseases rather than the combined effects of several diseases (James, 1974; Cooke, 1998). Often two or more pests or diseases occur together on the same crops and there are interactions between their effects on crop yield. Research on combined effects of several diseases on crop yield has shown that multiple infections may decrease yield more than (positive interaction), less than (negative interaction) or equal to (no interaction, additive) the sum of yield losses from individual diseases alone (Waller & Bridge, 1984; Johnson *et al*., 1986). Potato early dying is caused by a combination of the nematode *Pratylenchus penetrans* and the soil pathogen *Verticillium dahliae*; when they infect potato plants together they act synergistically to cause yield decreases of 25–50%, but infection with either alone has little or no effect on yield (Rowe *et al*., 1985; Francl *et al*., 1987; Wheeler *et al*., 1994). Other examples of positive interactions between pests and diseases in their effects on crop yield include sharp eyespot (*Rhizoctonia cerealis*) and the grain aphid (*Sitobion avenae*) on wheat (Wu *et al*., 1995), and brown rust (*Puccinia recondita* f.sp. *tritici*) and septoria blotch (*Septoria nodorum*) on wheat (Van der Wal *et al*., 1970). Negative interactions between pests and diseases in their effects on yield of potato have occurred between early blight (*Alternaria solani*) and verticillium wilt (*Verticillium dahliae*) (Harrison, 1974) and between *A. solani*, *V. dahliae* and the potato leaf-hopper (*Empoasca fabae*) (Johnson *et al*., 1986). However, yield loss studies have shown no interactions (i.e. additive losses)

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between effects on wheat yield of powdery mildew (*Blumeria graminis* f.sp. *tritici*) and brown rust (Bowen *et al*., 1991); between powdery mildew and stripe rust (*Puccinia striiformis* f.sp. *tritici*) (Zhou *et al*., 1995); or between brown rust, eyespot (*Tapesia yallundae*), sharp eyespot and tan spot (*Pyrenophora trichostoma*) (Wiese *et al*., 1984). When interactions occur, estimates of yield losses caused by several diseases made by addition of single disease yield-loss models are likely to be inaccurate, and combined disease yield-loss models should be used.

Stem canker (*Leptosphaeria maculans*) and light leaf spot (*Pyrenopeziza brassicae*), the two most important diseases on winter oilseed rape in the UK, often occur together on crops in southern England, although in Scotland only light leaf spot occurs. It was estimated that stem canker and light leaf spot caused yield losses of 3–29% and 8–29%, respectively, in the UK during the period 1987–95 (Fitt *et al*., 1997). Winter oilseed rape yield-loss models for stem canker alone and for light leaf spot alone in the UK have generally estimated losses in t ha^{-1}, either in relation to disease incidence (percentage of plants affected) on stems before harvest in England (Church & Fitt, 1995; Sansford *et al*., 1996) or the area under the disease progress curve (AUDPC) of light leaf spot severity on leaves in Scotland (Sutherland *et al*., 1995). There has been considerable variation in yield-loss coefficients (values of the slope of the regression lines) between sites and seasons, partly because absolute seed yield is affected by many factors other than disease. Yield-loss models for stem canker (blackleg), with losses expressed as percentage yield loss, have been produced in Australia (McGee & Emmett, 1977) and Canada (Hall *et al*., 1993), but it is not clear that they are relevant to the UK since both crop growth and disease development differ greatly between continents. The only percentage yield-loss models for the UK are those of Zhou *et al*. (1999) for stem canker (based on data from experiments with cvs Envol, Capitol and Lipton in southern England) and Su *et al*. (1998) for light leaf spot (based on data for cv. Envol in Scotland). However, no models have been developed to describe relationships between oilseed rape yield and these two diseases together. This paper investigates the combined effects of stem canker and light leaf spot on the yield of winter oilseed rape, and compares combined yield-loss models with the sum of individual yield-loss models for these two diseases.

Materials and methods

Data sets for constructing and testing models relating decrease in seed yield of winter oilseed rape to combined incidence/severity of stem canker and light leaf spot were obtained from field experiments at Rothamsted, southern England in 1992/93, 1993/94, 1994/95 and 1995/96, and at ADAS Boxworth, southern England in 1992/93. These data are stored in the Electronic Rothamsted Archive, with codes 93RRAW5, 94RRAW5, 95RRAW5, 96RRAW5 and 93AERAW1, respectively. The data from experiments at Rothamsted in 1992/93, 1994/95 and 1995/96 were used to construct the models, and those from Rothamsted in 1993/94 and ADAS Boxworth in 1992/93 were used to test them. These five data sets were selected because, in these experiments, stem canker and light leaf spot occurred together and both affected crop yield, whereas other diseases were absent, or present at low severity. The correlations between data for light leaf spot and stem canker were small in the three data sets used to construct the model, whereas they were greater in the two data sets used to test the model. The experiments were arranged in randomized block designs. At Rothamsted, they comprised three blocks of 25 plots in 1992/93 and 1993/94, three blocks of 16 plots in 1994/95, and four blocks of six plots in 1995/96. There were two blocks of 22 plots at Boxworth in 1992/93. The plot areas at Rothamsted were 75 m^2 in 1992/93 and 60 m^2 in 1993/94, 1994/95 and 1995/96; and at Boxworth 144 m^2 in 1992/93. The winter oilseed rape cultivar Envol, used in all experiments, was sown at Rothamsted on 28 August 1992 (after winter wheat), 18 September 1993 (after set-aside), 18 September 1994 (after set-aside) and 5 September 1995 (after winter wheat); and at Boxworth on 3 September 1992 (after winter wheat). The experiments at Rothamsted in 1992/93, 1993/94, 1994/95 and 1995/96 were inoculated with infected oilseed rape stem debris (baled after harvest the previous season) in October (approximately 10 kg debris per plot), and the experiment at Boxworth in 1992/93 was uninoculated.

Different disease epidemic patterns in each of the experimental plots were obtained using fungicides, with six to 22 different spray regimes. A mixture of iprodione plus thiophanate-methyl (as Compass) at 250/250 g a.i. with prochloraz (as Sportak 45) at 250 g a.i. in 200 L ha^{-1} was applied at Rothamsted in 1992/93 and 1993/94, and at Boxworth in 1992/93. There were 22 different spray treatments consisting of sequential applications to plots at monthly intervals; one series of treatments began in the autumn and finished progressively later, and the second series finished at harvest and started progressively earlier. Further details of these experiments are given by Sansford *et al*. (1996). Tebuconazole (as Folicur) was applied at Rothamsted in 1994/95 and 1995/96, either monthly from November to April at half-rate (125 g a.i. in 220 L ha^{-1}); once at full rate (250 g a.i. in 220 L ha^{-1}) in October, November, December, March or April; or twice at half-rate in October, November or December plus March; further details of these experiments are given by Fitt *et al*. (1998b). Control plots were unsprayed in all experiments.

In each of these experiments, 10 plants were sampled from each plot at approximately monthly intervals. Assessment dates for the stem canker and light leaf spot data (samples from March onwards) used to construct yield-loss models are shown in Table 1. Incidence (percentage plants with leaves or stems affected) and

Table 1 Seasons and sites of field experiments providing data used to construct or test equations relating winter oilseed rape yield loss to combined incidence or severity of stem canker and light leaf spot

Season	Site	Date of sowing	Date of harvest	Date of disease assessment[a]	Days after sowing	Days before harvest	Growth stage (GS)
1992/93	Rothamsted	28 August 1992	28 July 1993	17 March	201	133	3,5
				15 April	230	104	4,0
				12 May	257	77	5,8
				9 June	285	49	6,3
				7 July	313	21	6,3/6,4
1994/95	Rothamsted	18 September 1994	17 July 1995	20 March	183	120	3,0
				11 April	205	98	4,0
				10 May	234	69	4,5
				26 May	250	53	5,8
				20 June	275	28	6,3
				17 July	302	1	6,5
1995/96	Rothamsted	5 September 1995	30 July 1996	10 April	218	111	4,0
				20 May	258	71	5,7
				28 June	297	32	6,3
				17 July	316	13	6,5
1993/94	Rothamsted	18 September 1993	1 August 1994	4 May	228	89	4,3
				1 June	256	61	6,1
				29 June	284	33	6,3
				20 July	305	12	6,5
1992/93	Boxworth	3 September 1992	20 July 1993	17 March	195	125	2,05/3,3
				8 April	217	103	3,7
				7 May	246	74	4,9/5,4
				1 June	271	49	6,2
				28 June	298	22	6,4

[a]Disease assessments earlier in the season were not used to construct yield-loss models.

severity of stem canker and light leaf spot on leaves or stems were recorded. Stem canker severity assessments used a 0–4 scale (Hardwick *et al*., 1989; 0, no disease; 1, less than half the stem girdled by lesions; 2, more than half the stem girdled by lesions; 3, whole stem girdled and weakened by lesions; 4, plant dead) in all experiments. Light leaf spot severity on stems was assessed using this 0–4 scale at Rothamsted in 1994/95, and as percentage area of stem affected at Rothamsted in 1992/93, 1993/94 and 1995/96 and at Boxworth in 1992/93. Growth stages (GS) of the crop were recorded using the key of Sylvester-Bradley & Makepeace (1985). Plots were combine-harvested directly in July or August, and seed yields were recorded and adjusted to 90% dry matter.

Correlation and linear regression analyses were used to examine the relationships between yield loss and stem canker/light leaf spot and to establish critical point (CP) and AUDPC models between yield loss and combined stem canker and light leaf spot assessments for the different experiments. Interaction variables (stem canker × light leaf spot) were included in the linear regression analyses, both with and without logarithmic or square root transformations. AUDPCs were calculated from data on progress of stem canker or light leaf spot over several months using the trapezium rule:

$$\text{AUDPC} = \sum_{i=1}^{i=n-1} 0{\cdot}5(x_{i+1} + x_i)(t_{i+1} - t_i) \quad (1)$$

where t_i is the Julian day number, x_i is incidence or severity at assessment day i, and n is the number of assessment dates. Differences between CP and AUDPC models for different experiments were compared using linear regression analyses of position and parallelism.

Linear regression analysis and the *F*-test were used to validate models for relating percentage yield loss to combined and individual stem canker and light leaf spot assessments. Observed (y) and predicted (x) percentage yield losses were calculated, the linear regression equation $y = a + bx$ was calculated, and then the hypothesis $a = 0$, $b = 1$ was tested to compare the accuracy of the predictions made by combined or individual yield-loss models (Teng, 1985). The statistical package Genstat (Payne *et al*., 1993) was used for all analyses.

Results

Epidemics of stem canker and light leaf spot

Stem canker and light leaf spot occurred together in experiments at Rothamsted in 1992/93, 1993/94, 1994/95 and 1995/96, and at Boxworth in 1992/93 (Figs 1 and 2), but epidemic patterns differed between seasons and sites. Development of light leaf spot epidemics on leaves was similar in experiments at Rothamsted in 1992/93, 1993/94, 1994/95 and 1995/96, but different from that at Boxworth in 1992/93. At Rothamsted in

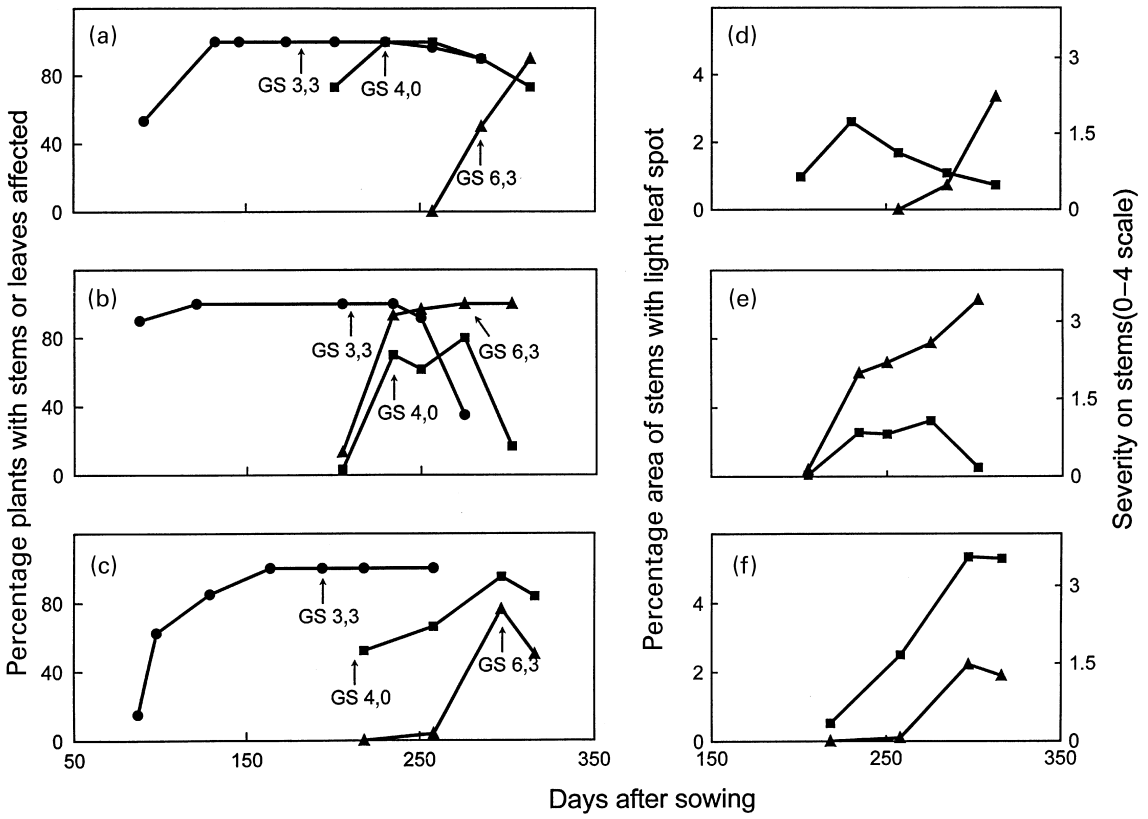

Figure 1 Changes in incidence (percentage of plants affected; a–c) and severity (d–f) of stem canker on stems (▲) and light leaf spot on leaves (●) or stems (■) in untreated plots of winter oilseed rape in field experiments at Rothamsted in 1992/93 (a, d); 1994/95 (b, e); and 1995/96 (c, f), which were used to construct combined yield-loss models. Severity of stem canker on stems in 1992/93, 1994/95 and 1995/96, and severity of light leaf spot on stems in 1994/95, were assessed using a 0–4 scale; in 1992/93 and 1995/96, severity of light leaf spot on stems was assessed as percentage area of stems affected.

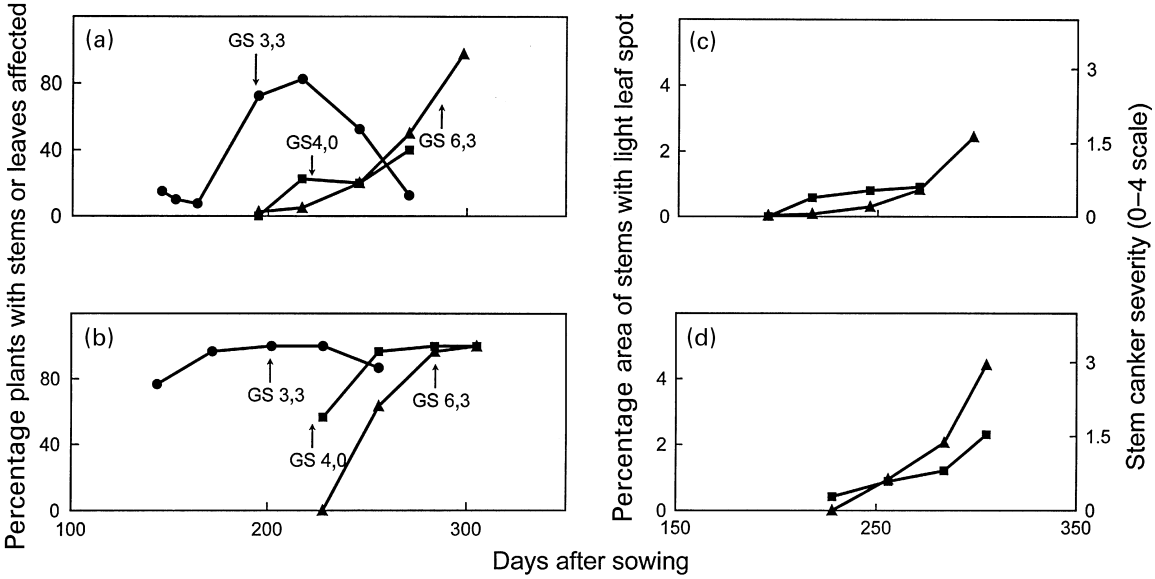

Figure 2 Changes in incidence (percentage of plants affected; a, b) and severity (c, d) of stem canker on stems (▲) and light leaf spot on leaves (●) or stems (■) in untreated plots of winter oilseed rape in field experiments at Boxworth in 1992/93 (a, c) and at Rothamsted in 1993/94 (b, d), which were used to test combined yield-loss models.

Table 2 Yields (t ha^{-1}) of plots with (maximum yield obtained) or without fungicide treatments in winter oilseed rape field experiments affected by both stem canker and light leaf spot

		Yield (t ha^{-1})		
Season	Site	No fungicide	With fungicide (maximum)	SED (df)
1992/93	Rothamsted	3·35	5·10	0·207 (48)
1994/95	Rothamsted	4·50	5·16	0·121 (35)
1995/96	Rothamsted	3·92	4·36	0·123 (16)
1993/94	Rothamsted	3·09	3·73	0·179 (52)
1992/93	Boxworth	3·85	4·75	0·230 (23)

1992/93 and 1995/96, light leaf spot (on stems) occurred earlier and was more severe than stem canker. At Boxworth in 1992/93, stem canker lesions developed most rapidly after 7 May (GS 4,9/5,4; 246 days after sowing; Table 1) and the percentage of plants affected increased to 98% by 28 June (GS 6,4). The increase in incidence and severity of stem canker after 7 May was similar to that of light leaf spot on stems in this season. Of the five experiments, stem canker occurred earliest and was most severe at Rothamsted in 1994/95; symptoms on stems were observed on 20 March (GS 3,0; 183 days after sowing) and incidence had reached 100% by 20 June (GS 6,3). Light leaf spot on stems occurred earliest and was most severe at Rothamsted in 1992/93, when 73% of plants were affected by 17 March (GS 3,5) and 100% by 15 April (GS 4,0). Maximum yields obtained in these experiments ranged from 3·73 t ha^{-1} at Rothamsted in 1993/94 to 5·16 t ha^{-1} at Rothamsted in 1994/95; percentage yield losses in untreated plots ranged from 10% at Rothamsted in 1995/96 to 34% at Rothamsted in 1992/93 (Table 2).

Relationships between percentage yield loss and stem canker or light leaf spot assessments on different dates

Coefficients of correlation between percentage yield loss and incidence or severity of stem canker or light leaf spot on different assessment dates at Rothamsted in 1992/93, 1994/95 and 1995/96 were calculated (Table 3). There were positive relationships ($P < 0·05$) between percentage yield loss and incidence or severity of stem canker from 9 June (GS 6,3) to 7 July (GS 6,4) in 1993, and from 10 May (GS 4,5) to 17 July (GS 6,5) in 1995, but only on 28 June (GS 6,3) in 1996. Yield loss was related ($P < 0·001$) to incidence or severity of light leaf spot from 17 March (GS 3,5) to 7 July 1993 (GS 6,4), with similar correlation coefficient (r) values (0·61–0·66) at each assessment date. Yield loss was related ($P < 0·02$) to incidence or severity of light leaf spot on 10 May (GS 4,5) and 26 May (GS 5,8) 1995, and on 10 April (GS 4,0) and 28 June (GS 6,3) 1996.

Models of relationships between percentage yield loss and combined stem canker and light leaf spot assessments

Data sets from experiments at Rothamsted in 1992/93, 1994/95 and 1995/96 were used to construct CP and AUDPC models relating percentage yield loss to incidence or severity of stem canker, light leaf spot (on stems) and their interactions by multiple linear regression (Table 4). An attempt was made to construct multiple-point (MP) models to describe the relationships between percentage

Table 3 Coefficients of correlation (r) between percentage yield loss of winter oilseed rape and incidence or severity of stem canker or light leaf spot on stems at different growth stages at Rothamsted in 1992/93, 1994/95 and 1995/96

		Stem canker				Light leaf spot				
	Date of disease assessment	Incidence		Severity		Incidence		Severity[a]		
Season	(Growth stage)	r	P	r	P	r	P	r	P	df
1992/93	17 March (GS 3,5)	–	–	–	–	0·66	<0·001	0·64	<0·001	40
	15 April (GS 4,0)	–	–	–	–	0·63	<0·001	0·66	<0·001	46
	12 May (GS 5,8)	–	–	–	–	0·64	<0·001	0·69	<0·001	52
	9 June (GS 6,3)	0·31	0·017	0·27	0·037	0·61	<0·001	0·59	<0·001	58
	7 July (GS 6,3/6,4)	0·71	<0·001	0·68	<0·001	0·63	<0·001	0·63	<0·001	64
1994/95	20 March (GS 3,0)	−0·03	0·91	−0·03	0·91	0·26	0·30	0·26	0·30	16
	11 April (GS 4,0)	0·40	0·07	0·44	0·05	0·47	0·03	0·36	0·11	19
	10 May (GS 4,5)	0·58	0·003	0·67	<0·001	0·48	0·02	0·45	0·026	22
	26 May (GS 5,8)	0·38	0·07	0·60	0·002	0·49	0·01	0·54	0·006	22
	20 June (GS 6,3)	0·42	0·01	0·50	0·002	0·03	0·85	0·13	0·45	34
	17 July (GS 6,5)	0·42	0·01	0·58	<0·001	0·13	0·46	0·11	0·54	34
1995/96	10 April (GS 4,0)	–	–	–	–	0·53	0·008	0·54	0·006	22
	20 May (GS 5,7)	0·06	0·79	0·18	0·41	0·23	0·29	0·45	0·029	22
	28 June (GS 6,3)	0·54	0·006	0·60	0·002	0·59	0·002	0·52	0·01	22
	17 July (GS 6,5)	0·21	0·32	0·18	0·41	0·14	0·50	−0·05	0·83	22

[a]Severity of light leaf spot on stems was assessed on a 0–4 scale at Rothamsted in 1994/95, and as percentage area of stems affected at Rothamsted in 1992/93, 1993/94, 1995/96 and at Boxworth in 1992/93.

Table 4 Equations describing relationships between percentage yield loss (ΔY) of winter oilseed rape and combined incidence or severity of stem canker and light leaf spot (stems) at Rothamsted in 1992/93, 1994/95 and 1995/96

Season	Model	Equation	R^2(%)[a]	P[b]	df	Parameter definition
1992/93	CP[c]	$\Delta Y = 0{\cdot}25 + 0{\cdot}093S_i + 0{\cdot}065L_i$	43·0	< 0·001	44	S_i, L_i or S_s, L_s = incidence or severity of stem
	AUDPC[d]	$\Delta Y = 1{\cdot}99 + 3{\cdot}13S_s + 3{\cdot}85L_s$	45·3	< 0·001	44	canker on 7 July and light leaf spot on 5 April
		$\Delta Y = 0{\cdot}26 + 0{\cdot}00098S_{ia} + 0{\cdot}0025L_{ia}$	40·4	< 0·001	44	S_{ia}, L_{ia} or S_{sa}, L_{sa} = AUDPC of incidence or
		$\Delta Y = 1{\cdot}56 + 0{\cdot}095S_{sa} + 0{\cdot}24L_{sa} - 0{\cdot}0020\ S_{sa}L_{sa}$	46·1	< 0·001	43	severity of stem canker from 12 May to 7 July and light leaf spot from 15 April to 9 June
1994/95	CP	$\Delta Y = 0{\cdot}02 + 0{\cdot}079S_i + 0{\cdot}069L_i$	30·5	0·008	21	S_i, L_i or S_s, L_s = incidence or severity of stem
		$\Delta Y = 2{\cdot}51 + 2{\cdot}73S_s + 4{\cdot}52L_s$	36·6	0·003	21	canker on 20 June and light leaf spot on 10 May
	AUDPC	$\Delta Y = -5{\cdot}16 + 0{\cdot}0019S_{ia} + 0{\cdot}0030L_{ia}$	36·0	0·004	21	S_{ia}, L_{ia} or S_{sa}, L_{sa} = AUDPC of incidence or
		$\Delta Y = -2{\cdot}58 + 0{\cdot}085S_{sa} + 0{\cdot}25L_{sa} - 0{\cdot}0011S_{sa}L_{sa}$	37·3	0·006	20	severity of stem canker from 26 May to 17 July and light leaf spot from 10 May to 20 June
1995/96	CP	$\Delta Y = 2{\cdot}14 + 0{\cdot}069S_i + 0{\cdot}048L_i$	25·8	0·017	21	S_i, L_i or S_s, L_s = incidence or severity of stem
		$\Delta Y = 2{\cdot}43 + 4{\cdot}36S_s + 2{\cdot}97L_s$	30·4	0·009	21	canker on 28 June and light leaf spot on 10 April
	AUDPC	$\Delta Y = -1{\cdot}97 + 0{\cdot}0033S_{ia} + 0{\cdot}00062L_{ia}$	31·8	0·007	21	S_{ia}, L_{ia} or S_{sa}, L_{sa} = AUDPC of incidence or
		$\Delta Y = 0{\cdot}40 + 0{\cdot}12S_{sa} + 0{\cdot}018L_{sa}$	41·5	0·001	21	severity of stem canker from 20 May to 17 July and light leaf spot from 10 April to 28 June

[a]Percentage variance accounted for.
[b]P value of F-test.
[c]Critical point model.
[d]Area under disease progress curve model.

yield loss and combined stem canker and light leaf spot assessments. However, MP models gave no improvement over CP models because there were strong correlations between successive disease assessments for both diseases. The results showed that the linear regressions were significant for all CP and AUDPC models ($P < 0{\cdot}017$). CP and AUDPC models for incidence or severity for experiments at Rothamsted in 1992/93, 1994/95 and 1995/96 accounted for 25–46% of the variance. The percentages of variance accounted for by AUDPC models for incidence or severity for the three experiments were greater than those for CP models, except for incidence in the 1992/93 experiment. The CP and AUDPC models for severity accounted for greater percentages of the variance than did CP and AUDPC models for incidence.

The differences in the models for incidence of stem canker and light leaf spot between experiments were compared using regression analyses of position and parallelism. There were no significant differences between CP models for all three experiments. Thus a general CP model for incidence was constructed, based on combined data from experiments at Rothamsted in 1992/93, 1994/95 and 1995/96:

$$\Delta Y = 0{\cdot}85 + 0{\cdot}079S_i + 0{\cdot}065L_i \quad (2)$$
$$(R^2 = 43{\cdot}7\%, P < 0{\cdot}001, 92\,\text{df})$$

where ΔY = percentage yield loss, S_i = incidence of stem canker at GS 6,3/6,4, and L_i = incidence of light leaf spot at GS 4,0/4,5. The fit of the general yield-loss relationship (Eqn 2) from the three experiments was compared to the fit of the individual yield-loss relationships derived from data for each experiment. The analyses indicated that there were no statistically significant differences between the general model and the individual models.

Comparison of the AUDPC models for incidence showed that there was no difference between models for Rothamsted in 1992/93 and 1994/95, but that the model for Rothamsted in 1995/96 was significantly different. Therefore, an AUDPC model for incidence was constructed, based on data from experiments at Rothamsted in 1992/93 and 1994/95:

$$\Delta Y = 0{\cdot}07 + 0{\cdot}00096S_{ia} + 0{\cdot}0026L_{ia} \quad (3)$$
$$(R^2 = 43{\cdot}6\%, P < 0{\cdot}001, 68\,\text{df})$$

where ΔY = percentage yield loss, S_{ia} = AUDPC of incidence of stem canker from GS 5,7–6,5, and L_{ia} = AUDPC of incidence of light leaf spot from GS 4,0–6,3. The fit of the general yield-loss relationship for AUDPC of incidence derived from data for these two experiments was compared to the fit of the individual yield-loss relationships derived from data for each experiment; the model derived from the combined data sets was not significantly different from the models for each experiment. However, the general model was significantly different from the model for AUDPC of incidence for Rothamsted in 1995/96. Since the severity of light leaf spot on stems was assessed using two different methods (on a 0–4 severity scale in 1994/95, and as percentage area of stem affected in 1992/93 and 1995/96), the differences between the models for combined severity of stem canker and light leaf spot for each of these experiments were not compared.

Validating yield-loss models for combined or individual stem canker and light leaf spot assessments

Two data sets (from Rothamsted in 1993/94 and Boxworth in 1992/93) were used to validate the CP and AUDPC yield-loss models for combined incidence of stem canker and light leaf spot. The differences between the lines produced

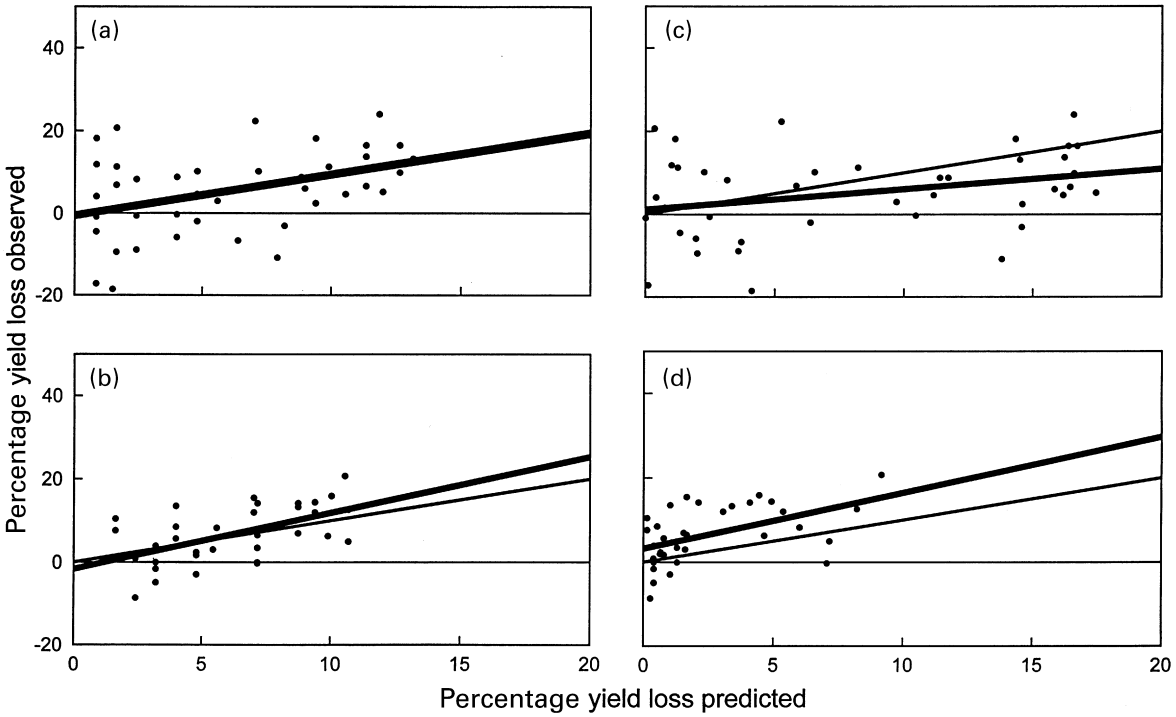

Figure 3 Comparison between percentage yield loss observed (y) and percentage yield loss predicted (x) by CP (a, b) or AUDPC (c, d) models for combined incidence of stem canker and light leaf spot (stem) on winter oilseed rape; regression lines (thick lines) for Rothamsted in 1993/94 (a, $y = -0{\cdot}74 + 0{\cdot}99x$, $R^2 = 14{\cdot}8\%$, $P = 0{\cdot}007$, 40 df; c, $y = 1{\cdot}14 + 0{\cdot}49x$, $R^2 = 7{\cdot}3\%$, $P = 0{\cdot}046$, 40 df) and Boxworth in 1992/93 (b, $y = -1{\cdot}64 + 1{\cdot}35x$, $R^2 = 30{\cdot}3\%$, $P < 0{\cdot}001$, 32 df; d, $y = 3{\cdot}22 + 1{\cdot}32x$, $R^2 = 23{\cdot}1\%$, $P = 0{\cdot}002$, 32 df). Thin line, $y = x$.

by regression of observed percentage yield loss (y) against predicted percentage yield loss (x) from models and line $y = x$ were compared using the F-test. There were no differences between the lines produced by regression of observed percentage yield loss at Rothamsted in 1993/94 (Fig. 3a) or Boxworth in 1992/93 (Fig. 3b) against percentage yield loss predicted from the CP model for incidence (Eqn 2) and the line $y = x$. However, there were significant differences ($P < 0{\cdot}05$) between the lines produced by regression of observed percentage yield loss at Rothamsted in 1993/94 (Fig. 3c) and at Boxworth in 1992/93 (Fig. 3d) against percentage yield loss predicted from AUDPC models for incidence (Eqn 3) and the line $y = x$. These results suggest that the CP model for combined incidence of stem canker and light leaf spot was more consistent than the AUDPC model for combined disease incidence.

All five of these data sets (from Rothamsted in 1992/93, 1993/94, 1994/95 and 1995/96, and from Boxworth in 1992/93) were used to evaluate and validate the use of the sum of the individual percentage yield-loss models for stem canker (Eqn 4; Zhou *et al.*, 1999) and light leaf spot (Eqn 5; Su *et al.*, 1998) for crops where both diseases were present:

$$\Delta Y = -1{\cdot}90 + 0{\cdot}27S_i (R^2 = 37{\cdot}7\%, 122\,\text{df}) \quad (4)$$

$$\Delta Y = -0{\cdot}57 + 0{\cdot}32L_i (R^2 = 63{\cdot}5\%, 84\,\text{df}) \quad (5)$$

where ΔY = percentage yield loss, S_i = stem canker incidence at GS 6,3/6,4, and L_i = light leaf spot incidence (percentage of plants with leaves affected) at GS 3,3. F-test results indicated that for each experiment there were differences between the lines produced by regression of observed percentage yield loss against percentage yield loss predicted by summing individual CP models for incidence of stem canker alone (Eqn 4) and light leaf spot alone (Eqn 5) and the line $y = x$; the percentage yield losses predicted from summed values from the individual models were always greater than observed percentage yield losses in these experiments where the diseases occurred together (Fig. 4). Direct comparison with other UK yield-loss models for light leaf spot alone or stem canker alone was not possible because in those models yield loss was expressed in t ha^{-1} rather than as percentage yield loss.

Discussion

Correlation analyses indicated that critical points for relating winter oilseed rape yield to occurrence of stem canker and light leaf spot (stems) were GS 6,3/6,4 (seed development) and GS 4,0/4,5 (flowering), respectively, when these two diseases occurred together in the same crops in southern England. These estimates of the critical point for stem canker were the same as estimates for relationships between percentage yield loss and stem canker alone (Zhou *et al.*, 1999). Seed development

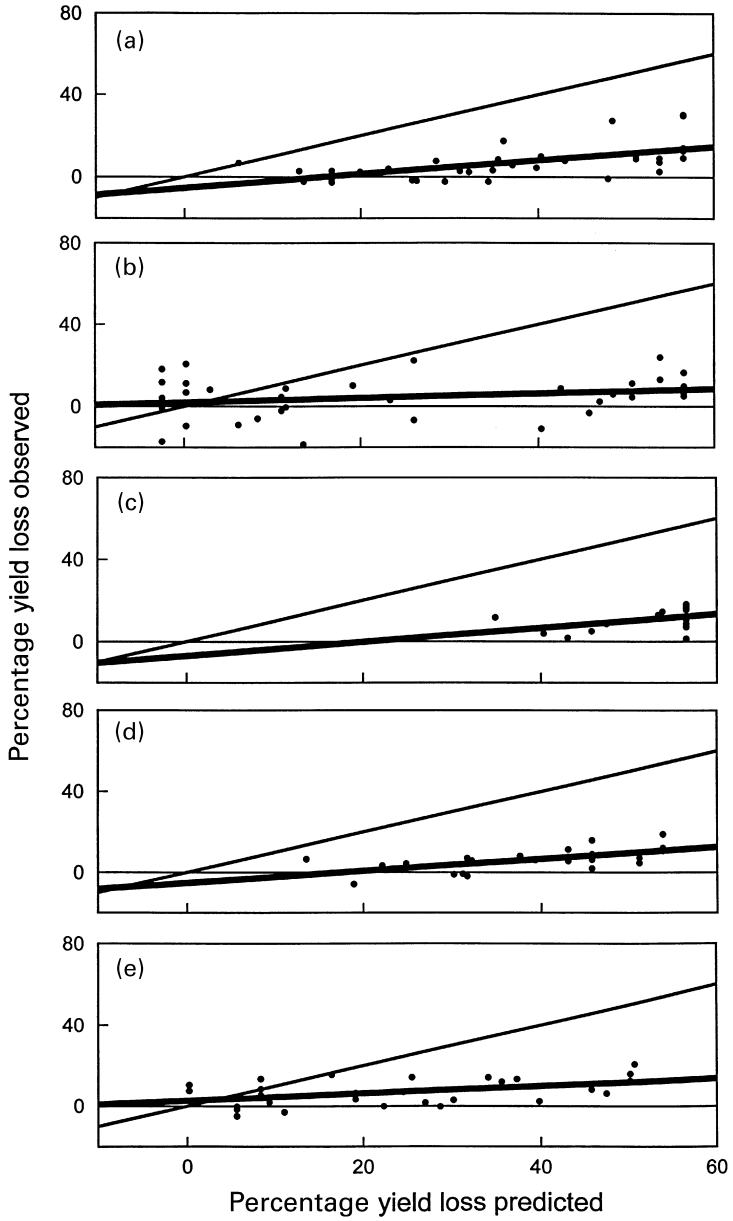

Figure 4 Comparison between percentage yield loss observed (y) and predicted (x) by summing individual CP models for incidence (percentage of plants affected) of stem canker alone and light leaf spot (leaves) alone on winter oilseed rape; regression lines (thick lines) for Rothamsted in 1992/93 (a, $y = -5{\cdot}28 + 0{\cdot}33x$, $R^2 = 34{\cdot}6\%$, $P < 0{\cdot}001$, 34 df); 1993/94 (b, $y = 1{\cdot}90 + 0{\cdot}11x$, $R^2 = 3{\cdot}4\%$, $P = 0{\cdot}15$, 34 df); 1994/95 (c, $y = -6{\cdot}92 + 0{\cdot}34x$, $R^2 = 13{\cdot}0\%$, $P = 0{\cdot}078$, 16 df); 1995/96 (d, $y = -5{\cdot}15 + 0{\cdot}30x$, $R^2 = 35{\cdot}7\%$, $P = 0{\cdot}001$, 22 df); and for Boxworth in 1992/93 (e, $y = 2{\cdot}69 + 0{\cdot}18x$, $R^2 = 19{\cdot}8\%$, $P = 0{\cdot}008$, 28 df). Thin line, $y = x$.

may have been the critical point for assessment of stem canker, because lesions that penetrate and damage stems at this growth stage would seriously impede transport of water and nutrients at a crucial phase in the production of yield. However, the estimates of the critical point for light leaf spot were later than estimates for relationships between percentage yield loss and light leaf spot alone (Su *et al.*, 1998). Su *et al.* (1998) suggested that the critical point for light leaf spot was the disease incidence (on leaves) at GS 3,3 (flower buds visible), using data (cv. Envol) from Scotland where light leaf spot occurs severely and stem canker does not occur. Their yield-loss model for light leaf spot (leaves) alone, based on assessment at GS 3,3, has predictive value and can be applied directly to guide fungicide application decision-making, because sprays to control light leaf spot can still be applied at GS 3,3. As lesions of light leaf spot on stems are generally superficial, they may not themselves cause much yield loss (Fitt *et al.*, 1998a), but their incidence may reflect the extent of damage to the leaves earlier in the season.

The correlation between light leaf spot (on stems) and yield loss may have occurred because the light leaf spot incidence on stems at GS 4,0/4,5 was related to earlier severity of damaging leaf disease epidemics. Therefore relationships between light leaf spot incidence at GS 3,3 (on leaves) and GS 4,0/4,5 (on stems) were analysed (Fig. 5). Light leaf spot on stems (GS 4,0/4,5) was related to light leaf spot on leaves (GS 3,3) ($P < 0{\cdot}001$) in the experiments at Rothamsted in 1993/94 and at Boxworth in 1992/93, but there was no significant relationship ($P > 0{\cdot}08$) between them in experiments at

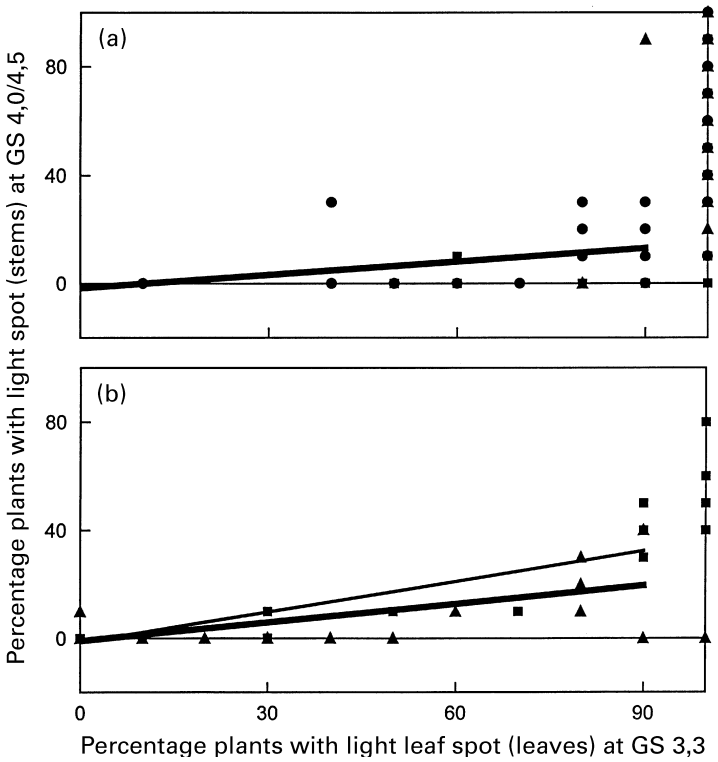

Figure 5 Relationships between light leaf spot on stems at GS 4,0/4,5 (y) and on leaves at GS 3,3 (x) at Rothamsted in 1992/93 (a, ●, $y = -1{\cdot}74 + 0{\cdot}16x$, $R^2 = 3{\cdot}4\%$, $P = 0{\cdot}22$, 16 df); 1993/94 (b, ■, thin line, $y = -1{\cdot}58 + 0{\cdot}38x$, $R^2 = 79{\cdot}2\%$, $P < 0{\cdot}001$, 25 df); 1994/95 (a, ▲); 1995/96 (a, ■); and at Boxworth in 1992/93 (b, ▲, thick line, $y = -0{\cdot}96 + 0{\cdot}23x$, $R^2 = 49{\cdot}9\%$, $P < 0{\cdot}001$, 27 df). Data from experiments at Rothamsted in 1992/93, 1994/95 and 1995/96 were used to construct the combined models, and those from Rothamsted in 1993/94 and from Boxworth were used to test them. Relationships were assessed by linear regression using data from all plots except values for 100% plants with light leaf spot on leaves at GS 3,3.

Rothamsted in 1992/93, 1994/95 and 1995/96, because the percentage of plants with light leaf spot on leaves in most plots reached 100% before GS 3,3 in these experiments. Further work is needed to investigate how the relationship between the development of light leaf spot and yield loss is affected by cultivar, seasonal and regional factors. Furthermore, these results suggest that the individual yield-loss model for light leaf spot on leaves has limitations when epidemics are very severe (e.g. when the percentage of plants with leaves affected reaches 100% before GS 3,3). However, in practice, commercial winter oilseed rape crops are not inoculated with infected debris, and farmers spray crops with fungicides before light leaf spot incidence reaches 100%.

The analyses indicated that the combined CP model was more consistent than the combined AUDPC model; the percentage yield loss predicted by the general combined CP model was similar to the observed percentage yield loss, and that predicted by the general combined AUDPC model was significantly different from that observed at Boxworth in 1992/93 and at Rothamsted in 1993/94. These results imply that the combined CP model for incidence can be applied to a greater range of crops at different sites in different seasons than the AUDPC model. A reason why both the combined disease AUDPC models and the light leaf spot AUDPC model of Sutherland *et al.* (1995) were not consistent between seasons may be that these models assumed that damage to the host was proportional to the amount of tissue affected and to the duration of the disease epidemics. Thus the model could not distinguish between early and late epidemics without applying weighting factors to assessments at different growth stages (James, 1974; Cooke, 1998). If disease occurring at different growth stages caused different amounts of yield loss, or patterns of epidemic development differed between sites or seasons, inconsistencies would occur in AUDPC models. Another reason for the inconsistency of AUDPC models may have been the quality of the light leaf spot data used to construct models. According to the data, at Rothamsted the incidence of light leaf spot on stems appeared to decrease greatly after 9 June in 1992/93, and after 26 May in 1994/95 (Fig. 1); although small decreases could be attributed to sampling error, in reality incidence on stems should not decrease as greatly at this time. However, the predictive accuracy of the AUDPC models for incidence or severity was greater than that of CP models in some experiments. It was not possible to compare differences in yield-loss models based on combined disease severity between experiments, or to evaluate their performance and consistency between seasons or sites, because the severity data for light leaf spot which were used to construct models were recorded by two different methods in different experiments. However, analyses indicated that models based on combined severity of diseases were better than those based on incidence (Table 4) and they merit further investigation.

Validation and evaluation of the models demonstrated that values for predicted percentage yield loss from the combined model for incidence were similar to those for observed percentage yield loss. The values for

predicted percentage yield loss summed from individual yield-loss models for incidence of stem canker and light leaf spot alone were greater than those for observed percentage yield loss. Values of the yield-loss coefficients (the regression slopes) of individual models for the incidence of stem canker or light leaf spot were greater than those of the stem canker or light leaf spot terms in the general combined yield-loss model. However, losses from light leaf spot in southern England, where it frequently occurs together with stem canker, are generally less than losses in Scotland (Su *et al*., 1998), where light leaf spot is more severe than in England and stem canker does not occur. As plots at Rothamsted were artificially inoculated with debris infected with light leaf spot, the incidence of the disease may have increased more rapidly at an earlier stage of the season than would have occurred under natural conditions. Furthermore, the growth stages for light leaf spot assessment used differed between the two models (Eqns 2 and 5). One possible reason for the difference in yield loss coefficient for stem canker between single and combined models was that patterns for the two diseases across plots within experiments were correlated because both disease epidemics were manipulated using the same fungicide applications; this made it difficult to attribute yield loss to each of the two diseases separately. This cannot account for all of the difference in the stem canker yield-loss coefficients between the two models, so it is likely that there was also a negative interaction between the two diseases. However, the only combined models with significant terms for interactions between stem canker and light leaf spot were the AUDPC models for severity from Rothamsted in 1992/93 and 1994/95 (Table 4). During calculations to develop combined models, there was generally no obvious improvement in accuracy when linear interaction terms were added. This suggests that the negative interaction was non-linear and hence was not detected by the analysis.

Harrison (1974) and Johnson *et al*. (1986) have reported that there are also negative interactions between the effects of early blight (*Alternaria solani*) and verticillium wilt (*Verticillium dahliae*) on yield of potato. Such negative interactions suggest that one disease cannot affect what the other disease has already damaged. Yield loss from one disease may depend on the incidence of the other disease (Harrison, 1974; Johnson *et al*., 1986). Therefore, if there are interactions between effects of several diseases on yield, the individual yield-loss models cannot be used. Furthermore, combined disease yield-loss models cannot be used when the diseases occur alone, or one of them is not severe. Knowledge of interactions between effects of diseases on yield loss is essential for decision-making for management of diseases occurring together, as stem canker and light leaf spot do on winter oilseed rape in much of southern England.

This knowledge can be used to improve yield-loss models for these two diseases, as a component of a decision-support system for integrated management of diseases on winter oilseed rape in the UK. A suite of yield-loss models could be developed, with different parameters for different cultivars and different regions of the UK; the combined stem canker and light leaf spot yield-loss model would be particularly applicable to southern England, where the two diseases occur together. However, these yield-loss models relate to assessments of light leaf spot and stem canker in spring, whereas decisions about application of fungicides to control these diseases need to be made in the autumn, some 6 months earlier. For these yield-loss models to be incorporated into a decision-support system, it would be necessary to combine them with models for autumn predictions of the spring incidence of stem canker and light leaf spot. To achieve this, it will be necessary to establish relationships between the incidence of phoma leaf spot (*L. maculans*) in the autumn and of stem canker in the spring, and between the incidence of symptomless light leaf spot infection in the autumn and of light leaf spot on leaves or stems in the spring.

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