Neth. J. Pl. Path. 97 (1991) 275-288

An advisory model for control of Puccinia recondita in winter wheat

R.A. DAAMEN

Research Institute for Plant Protection (IPO-DLO), P.O. Box 6700 GW Wageningen, the Netherlands

Accepted 29 July 1991

Abstract

Epidemics of *Puccinia recondita* and resulting yield loss of winter wheat were studied in field experiments over three seasons in the Netherlands. Results are reported and used to construct an advisory model for control of brown rust, based on rust monitoring. If the fraction of leaves with rust (I) at a certain development stage is determined, the average number of rust sori per leaf (M) was estimated by: $M = EXP(1.84 + 1.39ln(ln[1/(1-I)])$. The final number of sori per leaf (Mf) at early dough was forecast by an exponential growth: $Mf = M \cdot EXP(RGR \cdot t)$. The relative growth rate (RGR) averaged 0.163/day and the forecasting period, t, until early dough, was derived from published data. The forecast number of sori-days per leaf (S, AUDPC-value) was then obtained by: $S = (Mf-M)/RGR$. Yield loss (kg/ha) by brown rust was 1.15 times the number of sori-days per leaf at low rust intensities. The efficacy of the fungicides used was 85%. The forecast avoidable yield loss (L, kg/ha) was calculated by: $L = 0.85\ (1.15\ S)$. Economic thresholds for brown rust control at different development stages are given for Dutch wheat fields at a cost level of 270 kg/ha for one fungicide application.

Additional keywords: Triticum aestivum, brown rust, monitoring, epidemiology, yield loss, disease management.

Introduction

The yellow rust (*Puccinia striiformis* Westend.) epidemics of 1975 and 1977 in the Netherlands initiated the development of a computer-based advisory system for control of yellow rust (Rijsdijk, 1983). However, most farmers replaced the yellow rust susceptible cultivars with moderately susceptible and resistant cultivars in 1978. An expansion of the advisory system became of vital importance to avoid calendar spraying for other diseases and pests and thereby maximize the economic benefits of new fungicides and insecticides in the rapidly intensifying wheat cropping systems. In 1980 the advisory system was expanded with a model for control of brown rust (*Puccinia recondita* Rob. ex Desm.) using data originating from research on yellow rust (Rijsdijk et al., 1989). The brown rust epidemics of 1981 and 1983, in which 82 and 93 percent, respectively, of surveyed fields were rusted (Daamen et al., in prep.), stressed the importance of brown rust and gave the impetus for additional research.

The purpose of the research programme was to construct an advisory model for brown rust control. Brown rust epidemics and consequent yield losses were studied in field experiments during three cropping seasons. This paper reports results of the field experiments and the construction of an advisory model.

Materials and methods

Experiments. The field experiments were located on marine clay soils on the farms 'De Kandelaar' in 1983-84 and 1984-85 and on the 'Van Bemmelenhoeve' in 1985-86. After the harvest of ware potatoes and seedbed preparation, 130 kg ha^{-1} winter wheat was sown at a row distance of 17 cm on 31 October, 14 November and 21 October in 1983, 1984 and 1985, respectively. In each experiment, the nitrogen in the soil was supplemented to 200 kg N ha^{-1}. Plot size was 4 × 22, 6 × 8 and 6 × 10 m in the three years, respectively, from which 2 × 19, 4 × 6 and 3.5 × 6 m plots, respectively, were combine-harvested at the end of August or early September. Grain yields were standardized at 16% moisture and 1000 kernel weights were determined.

Treatments. In 1983, the cultivars Okapi and Swifta were sown in adjacent fields. In 1984, cv. Okapi was sown and in 1985 the cvs Arminda and Saiga were sown in a split-plot design, with cultivars as main plots. The cultivars Okapi, Arminda and Saiga were susceptible to brown rust, while Swifta was very susceptible, according to the Dutch descriptive list of cultivars.

Approximately 0.5×10^6 rust spores m^{-2} in 50 cc water with 100 ppm Tween80 were applied twice in May, using a propane-pressurized backpack sprayer. In 1984, a mixture of brown rust strains, isolated in 1971 ('classical') and isolated from cv. Flamingo in 1961 were used (Zadoks, 1966). In 1985, a mixture of isolates from cv. Felix (1960), Okapi (1981) and Arminda (1981) which were virulent on cv. Okapi were used (R.W. Stubbs, pers. comm.). In 1986, cv. Arminda was inoculated with a virulent isolate from Arminda and cv. Saiga was inoculated with a virulent isolate from cv. Felix; the isolates were avirulent to the opposing cultivar.

The fungicide triadimefon (0.5 kg ha^{-1} Bayleton) was used to modify the brown rust epidemics. Treatments in each experiment were: (1) uninoculated and unsprayed check (1983-84 excepted), (2) inoculated, (3) inoculated and complete control by 4-5 fungicide treatments, (4) different treatments on inoculated plots comprising single fungicide applications at different development stages. The experiments had 4 replicates and all plots were treated with herbicides, aphicides and a selective mildew fungicide, ethirimol (Milgo E, 1 liter ha^{-1}), when necessary.

Disease assessments. From the start of the epidemics, samples of 20 culms per plot were taken fortnightly and the crop development stage was recorded using the decimal code (DC) (Zadoks et al., 1974). On each fully expanded green leaf, assessments were made of the number of brown rust sori per leaf, the number of powdery mildew (*Erysiphe graminis* DC. ex Merat) pustules per leaf and the percentage leaf area infected, excluding chlorosis, by *Mycosphaerella graminicola* (Fuckel) Schroeter (stat. con. *Septoria tritici*) and/or *Monographella nivalis* (Schaff.) Müller (stat. con. *Microdochium nivalis* ≡ *Fusarium nivale*). Assessments were averaged for each leaf position, thus $\overline{m}$ is mean number of brown rust sori per leaf in a leaf layer. The mean disease intensity in the canopy of leaves was obtained by averaging over the leaf layers (M, mean number of sori per leaf in the canopy).

Statistics. AUDPC-values were calculated from the mean disease intensities in the canopy of leaves for each disease and were expressed as sori-days, pustule-days and percent-days for brown rust, powdery mildew and leaf blotch, respectively. Treatment effects were tested by analysis of variance following log transformation to stabilize variances, where necessary. Yields were regressed on the AUDPC-values of the diseases, taking the experimental design into account. If polynomials indicated significant deviations from linearity, a negative exponential function (Madden et al., 1981) was fitted to the data by a direct optimization:

$$Y_{ij} = a_i - b\,(1 - e^{-X_{ij}/c}) - d \cdot \text{covariate}_{ij} + e_{ij} \qquad (1)$$

in which Y_{ij} is plot yield in kg ha^{-1} and X_{ij} is the number of sori-days of brown rust per leaf and covariate$_{ij}$ represents one or more other diseases at block i and treatment j. Brown rust assessments of the inoculated, unsprayed plots were used to determine additional epidemiological features of brown rust as discussed below. It is stressed that the experiments were not, a priori, designed for these estimations.

The sample variance of the number of sori per leaf (Var(m)) was described in relation to the mean number of sori per leaf $\overline{m}$ in leaf position k by regression of the log transformed model (Taylor, 1961):

$$\ln(\text{Var}[m]_k) = a + b \ln(\overline{m}_k) \qquad (2)$$

The vertical distribution of brown rust in the canopy was described by a power function (Daamen, 1989). The cumulative number of sori per leaf divided by the total number of sori per culm (Y) was analyzed in relation to the cumulative leaf area divided by the total leaf area per culm (X). Both variates were calculated from top to bottom of the canopy and the profile parameter b was estimated by a direct optimization of the model:

$$Y = X^b \qquad (3)$$

The relation between the mean number of brown rust sori per leaf, averaged over the canopy of leaves (M), was described in relation to the incidence of brown rust in the canopy (I, fraction rusted leaves) by regression of the double log transformed model (Nachmann, 1981):

$$\ln(M) = a + b \ln(\ln[1/(1 - I)]) \qquad (4)$$

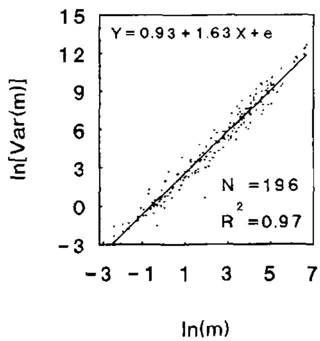
Relative growth rates of brown rust (RGR) were calculated from mean number of sori per leaf in the canopy (M) at two sequential assessment dates t1 and t2 and the time interval t in days by:

$$RGR = (\ln[M_{t2}/M_{t1}])/t \qquad (5)$$

In these analyses the effects of years, cultivars, development stages and, in case of Eq. 2 also leaf layers, on the parameter estimates were tested by analysis of variance. Development stage was then represented by a factor with three levels: DC $<$ 60; 60 $<$ DC $<$ 70 and DC $>$ 70. Genstat 5 was used for all analyses.

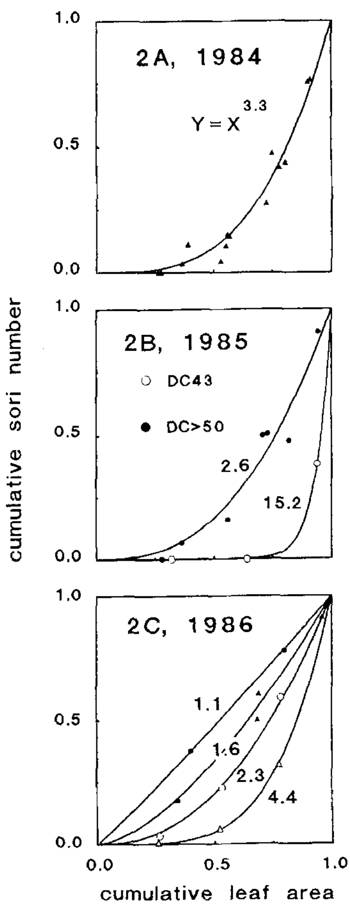
Results

Brown rust sampling. The sample variance of the number of sori per leaf depended on the mean number of sori per leaf in a leaf layer (Fig. 1, Eq. 2). Years, cultivars, development stages and position of the leaf layer had no significant effect, though the model underestimated the sample variance at very low (< 0.1 sori/leaf) rust intensities. To develop optimal sampling schemes for rust monitoring, the vertical distribution of brown rust in the canopy also needs to be considered. Brown rust profiles are shown in Fig. 2 (Eq. 3). In 1984, neither the cultivars Okapi and Swifta nor the development stages affected the estimates (b = 3.3, Fig. 2a). In 1985, the profile parameter was extremely large (15.2) early in the season (DC 43) (Fig 2b). Because of the artificial inoculations made in May, brown rust was only present on the two lowest leaf layers. Later in the season, the profile became less steep (b = 2.6) than in 1984. In 1986, the profile of brown rust was steeper in Arminda than in Saiga, and it was steeper during flowering than during ripening (Fig. 2c). The profile was nearly uniform (b = 1.1) in Saiga during ripening. If the highest estimate is neglected (b = 15.2, being the result of artificial inoculation), the average of b was 2.9, and the variance of b was 1.0, over



▲

Fig. 1. Sample variance (Var(m), log transformed) of the number of sori per leaf in relation to mean sori number ($\overline{m}$, log transformed) per leaf layer.
Standard errors of the parameters are 0.07, 0.02 and 0.69, respectively.
Each dot represents a sample of 20 leaves in a leaf layer.



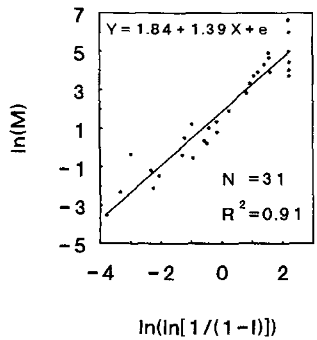
▶

Fig. 2. Brown rust profiles in 1984, 1985 and 1986. Cumulative number of sori in relation to cumulative leaf area, both calculated from top to bottom of the canopy and totals were standardized at unity. In Fig. 2a,b an average profile was estimated, see text. Entries are estimates of b in: $Y = X^b$. In Fig 2c: each line is the estimated profile in four samples of 20 tillers, each dot represents the data from the leaf layers; open triangles, Arminda DC61; closed triangles Arminda DC70-80; open circles, Saiga DC61; closed circles, Saiga DC70-80.

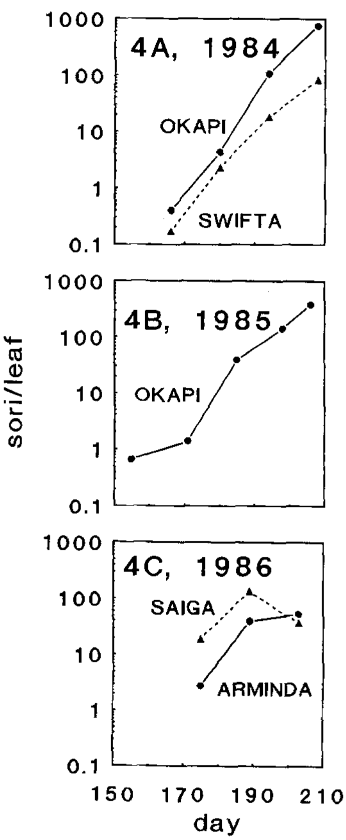
the different experiments. As b is an estimate of the brown rust intensity in the lowest part of the canopy (Daamen, 1989), the intensity there is about two to three times the average intensity in the canopy. Estimates of b decreased with development stage in each year but not significantly ($P > 0.05$), and cultivars did not have a significant effect on b. Though this would suggest that an average profile of brown rust may be assumed in order to develop an optimal sampling procedure, it is clear that deviations may occur (Fig. 2c).

In the advisory system in the Netherlands, incidence sampling (James and Shih, 1973) is used instead of a direct estimation of the number of sori per leaf. Years, cultivars and development stages had no significant effect on the incidence-severity relationship (Fig. 3, Eq. 4). The estimated relation is comparable to that established by James and Shih (1973). They estimated a brown rust severity of 0.55 to 0.85 percent at 50% incidence, while here the average number of sori per leaf was 2.9 to 5.0 (average 3.8) at an incidence of 50% (Fig. 3).

Brown rust epidemics. Growth of the brown rust population in the inoculated plots without fungicide application is shown in Fig. 4. In 1984 brown rust intensity was consistently lower in the more susceptible cv. Swifta than in cv. Okapi. The old brown rust strains employed presumably did not contain a strain highly virulent to Swifta.



▲ Fig. 3. Mean number of sori per leaf (M, log transformed) in the canopy in relation to brown rust incidence (I, the fraction of leaves with rust, double log transformed). Standard errors of the parameters are 0.14, 0.08 and 0.79, respectively. Each dot represents four samples of 20 tillers, including 12 data of other experiments during 1982-86.



▶ Fig. 4. Mean number of sori per leaf (M, ^{10}log scale) in time (Julian day) observed in the inoculated, non sprayed plots of the experiments in 1984-86. Each dot represents four samples of 20 tillers.

Table 1. Calculated relative growth rates (RGR, day $^{-1}$) of brown rust in different experiments and development stages (DC).

Year	Cultivar	DC	RGR	Year	Cultivar	DC	RGR
1983	Okapi	69-75	0.13	1984	Okapi	49-63	0.12
		75-83	0.10			63-71	0.24
	Swifta	69-75	0.08			71-77	0.14
		75-83	0.07		Swifta	49-63	0.16
1983	Okapi	71-75	0.28			63-71	0.15
	Swifta	71-75	0.14			71-77	0.11
1983	Arminda	69-73	0.24	1985	Okapi	43-53	0.05
1983	Citadel	59-65	0.32			53-67	0.24
		65-71	0.10			67-75	0.10
		71-81	0.27			75-77	0.13
1983	Minaret	57-71	0.19	1986	Arminda	65-71	0.25
		71-85	0.28			71-81	0.02
					Saiga	65-71	0.16
						71-81	−0.09

The epidemic of 1985 in Okapi was comparable to that of 1984. Unlike 1984 and 1985, the growth of brown rust during ripening was smaller in 1986. Brown rust intensity even decreased in Saiga due to a rapid leaf senescence. Maximum number of sori per leaf observed was about 1000 (Okapi in 1984), without an indication of reaching a maximum carrying capacity. Therefore an exponential growth of brown rust (Eq. 5) instead of a logistic growth was assumed. Calculated relative growth rates, including those of five experiments from 1983, are given in Table 1. Years, cultivars or development stages did not affect the growth rates significantly. If the negative growth rate, observed in Saiga in 1986 due to rapid leaf senescence is neglected, the growth rate averaged 0.163 day $^{-1}$ (sd: 0.081). Thus, brown rust intensity per leaf increased on average a tenfold per fortnight. Comparable rates of apparent infection during flowering and ripening in Louisiana are reported by Subba Rao et al. (1990). Those reported by Spitters et al. (1990) are a twofold higher but lie within the range observed.

Treatments, yields and diseases. Yields and the AUDPC-values of the diseases are given in Table 2. Brown rust predominated in all experiments. In 1984 speckled leaf blotch (*S. tritici*) and in 1985 snow mould (*M. nivalis*) were important together with brown rust. At ripening in 1985, a moderate infestation with ear blight (*Fusarium* spp. and *M. nivalis*) was recorded. Powdery mildew was of minor importance in 1984 and 1985. In 1986 diseases other than brown rust were virtually absent.

Four to five applications of triadimefon nearly eliminated brown rust but not the other diseases (Table 2). The efficacy of triadimefon to control brown rust was estimated by comparing the resulting number of sori-days at a single fungicide application, with the number of sori-days in the unsprayed plots. The efficacy was lowest during tillering-shooting because the fungicide persist circa three weeks and brown rust developed afterwards. The efficacy tended to be highest during booting-flowering (Table 3, DC45-67). The efficacy was low in Saiga at flowering (DC61-67), because the

Table 2. Treatments, yields and disease intensities in the experiments of 1984, 1985 and 1986. Values in a column (averages of four replicates) followed by different letters differ significantly according to the T-method.

1984

Treatments	Yield tonne/ha		Sori-days brown rust		Percent-days leaf blotch[b]		Pustule-days mildew	
1 2 3 4 5 6 7[a]	Okapi	Swifta	Okapi	Swifta	Okapi	Swifta	Okapi	Swifta
I I – – – – –	6.0d	6.6e	11328d	1371b	269b	394b	57bc	81b
I I T T T T T	8.5a	8.7a	117a	20a	173a	204a	14a	10a
I I T – – – –	6.1d	6.8de	10034d	1394b	213ab	409b	37ab	57ab
I I – – T – –	7.4b	8.1b	1342b	205a	208ab	291ab	23ab	23a
I I – – – T –	7.5b	7.6c	1380b	318a	258b	350ab	67bc	47ab
I I – – – – T	6.7c	7.2cd	3706c	536a	224b	369ab	91c	51ab

[a] I is inoculation, T is triadimefon application, 3...7 are dates: 3 and 18 May, 15 June, and 4 and 16 July, respectively.
[b] *S. tritici*.

1985 Okapi

Treatments 1 2 3 4 5 6[a]	Yield tonne/ha	Sori-days brown rust	Percent-days snow mould[b]	Pustule-days mildew	Glumes/ear ear blight
– – – – – –	6.0bcd	3726c	232b	44b	5.8a
I – – – – –	5.4d	4045c	406bc	36ab	5.7a
I I – – – –	5.4d	4971c	487c	77b	5.6a
– I T T T T	7.6a	83a	108a	33ab	4.6a
– I – – – –	5.9dc	3391c	235b	75b	4.7a
I I T – – –	6.2bc	2786c	274bc	25a	4.7a
I I – T – –	5.9cd	2591c	365bc	39ab	6.0a
I I – – T –	6.1bc	899b	320bc	43b	5.3a
I I – – – T	5.5cd	2491c	440c	51b	5.5a
I I – – F –	6.6b	761b	246b	35ab	4.0a

[a] I is inoculation, T (triadimefon) and F (fenpropimorph) are fungicide applications, 3,4,5,6 are dates 25 May, 19 June and 5 and 17 July, respectively.
[b] caused by *M. nivalis*.

1986

Treatments	Yield tonne/ha		Sori-days brown rust	
1 2 3 4 5 6[a]	Arminda	Saiga	Arminda	Saiga
– – – – – –	8.0b	7.3b	265a	1397bc
I I – – – –	7.4c	5.9d	1001b	2396d
I – T T T T	8.6a	8.7a	23a	284a
I I – T – –	8.1b	6.7c	391a	1866c
I I – – T –	8.6a	8.2a	157a	1143b

[a] 1 and 2 are inoculations (I), 3, 4, 5, 6 are applications of triadimefon (T) on 16 and 29 May and on 16 and 30 June, respectively.

Table 3. Estimated efficacy of triadimefon at different development stages.

Experiment		Development stages			
		25-35	45-55	61-67	71-76
1984	Okapi	11	88	88	67
1984	Swifta	0	85	77	61
1985	Okapi	44	48	82a	50
1986	Arminda	61	–	84	–
1986	Saiga	22	–	52	–

[a] The fungicide fenpropimorph rated 85%.

brown rust intensity decreased in the unsprayed plots due to rapid leaf senescence (Fig. 4). After a fungicide application, the number of sori per leaf generally did not decrease, but remained stable for approximately three weeks, after which it increased again. An application during heading-flowering would therefore be an effective stra-

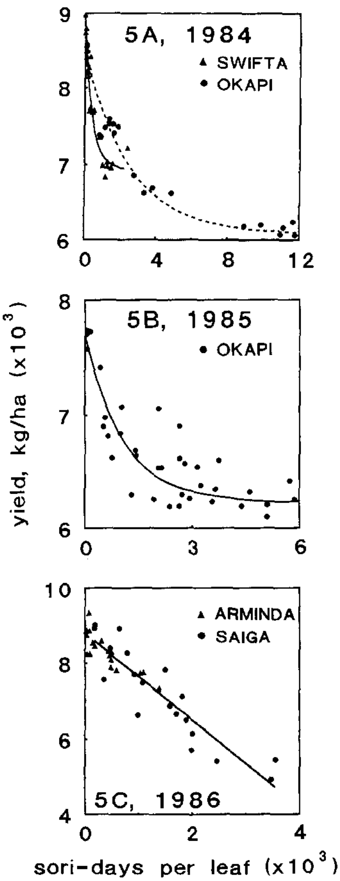


Fig. 5. Plot yield in relation to number of sori-days of brown rust per leaf in three experiments, adjusted for experimental design and covariates. Estimated relations are given in Table 4.

Table 4. Estimated yield loss relations. Y in kg ha^{-1}, X in sori-days of brown rust per leaf, see equation 1.

Experiment		Relation	Standard errors			
			a	b	c	e
1984	Okapi	$Y = 8477 - 2394\,(1 - e^{-X/2565}) + e$	120,	130,	396,	205
	Swifta	$Y = 8956 - 2010\,(1 - e^{-X/414}) + e$	151,	162,	76,	205
1985	Okapi	$Y = 7720 - 1489\,(1 - e^{-X/1079}) + e$	255,	173,	289,	257
1986	Arminda & Saiga	$Y = 8780 - 1.13\,X + e$	260,	0.12,	–,	480

tegy. At that time, the number of brown rust sori was still low, and after three weeks, the time left for growth of the brown rust population was short.

Yield loss. Plot yields of the experiments were analyzed in relation to the number of sori-days of brown rust per leaf (Eq. 1, Fig. 5 and Table 4) and the other diseases (Table 2), adjusted for the experimental design. In 1984 and 1985, the yield loss relation was described by a negative exponential relation and in 1986 by a linear relation. In 1984, the yield loss relation differed for the cultivars Okapi and Swifta ($P < 0.05$), while in 1986, cv. Arminda and Saiga showed similar relations ($P > 0.05$). Of the other diseases (Table 2), only snow mould in 1985 had a significant effect on yield (2.2 kg$\cdot$ha$^{-1}\cdot$percent-day$^{-1}\cdot$leaf^{-1}, SE = 0.4). To interprete the yield loss due to brown rust, the maximum observed loss and the yield loss per sori-day at low brown rust intensities (if X approaches zero, yield loss per sori-day per leaf approaches b/c, Eq. 1) are given in Table 5. It is clear that the maximum yield loss varied. For example, maximum yield loss attributed to brown rust was lower in 1984 and 1985 when *S. tritici* and *M. nivalis* were also important diseases, while yield loss was high in 1986 in Saiga

Table 5. Estimated maximum yield loss and estimated yield loss per sori-day at low brown rust intensities.

Experiment		Maximum loss		Loss rate at low intensity	
		kg/ha	%	kg/(ha.sori-day)	%
1984	Okapi	2394	28	0.93	0.011
	Swifta	2010	22	4.86	0.054
1985	Okapi	1489	19	1.38	0.018
1986	Arminda	1560[a]	18	1.13	0.013
	Saiga	4011[a]	46		

[a] Observed loss, linear relation does not indicate a maximum (Fig. 5).

when other diseases were negligible and the yield loss did not even reach a maximum level. Brown rust appears late in the ontogeny of the crop. Thus the maximum loss by brown rust presumably depends on other constraints affecting the crop. An average maximum yield loss of 30% is a reasonable estimate for forecasts in the Netherlands. A maximum loss of 30% fits well within the range of maximal losses reported in the literature (Bajwa et al., 1986; Subba Rao et al., 1989; Spitters et al., 1990; Seck et al., 1988). In the Netherlands, farmers will certainly aim at avoiding the maximum loss, since the cost of a fungicide application is equivalent to about three percent yield. Therefore, the exact maximum yield loss is, from the viewpoint of practical disease management, not as relevant as the yield loss per sori-day at low brown rust intensities (Table 5). This loss rate was fairly constant over the years, except in Swifta in 1984 which could indicate that Swifta is less tolerant to brown rust than the other cultivars. However, Swifta was relatively severily attacked by *S. tritici* compared to Okapi (Table 2). *S. tritici* did not show a significant effect on yield, being confounded with brown rust, so the apparent high brown rust loss rate in Swifta is presumably partly confounded with losses due to *S. tritici*. Analysis of data of 1984, using a single yield loss relation to describe yield loss in both cultivars, showed the covariate *S. tritici* to have a significant effect on yield (1.5 kg $ha^{-1} \cdot$ percent-$day^{-1} \cdot leaf^{-1}$, SE: 0.6). The loss rate at low brown rust intensities was then 1.3 kg ha^{-1}, which is comparable with the estimates in the other years. However, no definite interpretation can be given for the high loss rate observed in Swifta. Therefore, the estimate for Swifta was excluded. The loss rate due to brown rust averaged 1.15 kg $ha^{-1} \cdot$ sori-$day^{-1} \cdot leaf^{-1}$ (SE: 0.22) at low brown rust intensities. Unfortunately, a direct comparison of this estimate with literature data (Burleigh et al., 1972; Buchenau, 1975; Wellings et al., 1985; Subba Rao et al., 1989; Seck et al., 1988) is not possible.

Yield component. Yields were regressed on thousand kernel weights (Table 6). Yield loss was mainly caused by a reduction of the thousand kernel weight at an estimated kernel number of 20-23 thousand$\cdot m^{-2}$. However, in 1984 and in Saiga in 1986, the regressions did not pass through the origin, indicating that the number of kernels$\cdot m^{-2}$ was also reduced. Whether more kernels at low thousand kernel weights were lost during combine-harvesting or whether the diseases reduced the kernel number remains unclear.

Table 6. Yield (Y, g/m^2) in relation to thousand kernel weight (X, g/1000) in the experiments. Given are estimates of the relation: $Y = a + b \cdot X$ (standard errors between brackets).

Experiment		a g/m^2		b $1000/m^2$		Error g/m^2	R^2
1984	Okapi	−167	(51)	23	(1)	19	0.94
	Swifta	−233	(66)	22	(2)	28	0.90
1985	Okapi	−130	(69)ns	21	(2)	33	0.75
1986	Arminda	14	(11)ns	20	(3)	25	0.75
	Saiga	−202	(88)	21	(2)	41	0.86

ns = not significant ($P > 0.05$).

Advisory model. The information obtained was used to construct an advisory model based on disease monitoring. In spring, temperature is relatively low and diseased leaves are replaced by new leaves during stem elongation. The possibility of outbreaks of brown rust is therefore negligible and monitoring is not necessary. This conforms with the epidemics reported by Subba Rao et al. (1989). Crops need to be monitored after the final leaf has appeared (DC39). Then the mean number of sori per leaf (M) in the canopy and the development stage of the crop (DC) are to be determined. M can be monitored directly or it can be estimated from the fraction of full-grown leaves in the canopy with brown rust I by (Eq. 4, Fig. 3):

$$M_{DC} = e^{1.84 + 1.39\ln(\ln[1/(1 - I)])} \tag{6}$$

The brown rust epidemic is forecasted by an exponential growth up to early dough (DC83). The time in days (t_{DC}) from development stage DC45, DC55, DC61, DC65, DC71 and DC 73 until DC83 is 46, 40, 35, 32, 27, and 22.5 days, respectively (Reinink et al., 1986). The relative growth rate (RGR) averaged 0.163. Thus, the final number of sori (M_{83}) at DC83 is estimated by (Eq. 5):

$$M_{83} = M_{DC} \cdot e^{RGR \cdot t_{DC}} \tag{7}$$

The forecasted number of sori-days (S) is obtained by integration of equation (7) over the time interval until DC83:

$$S = (M_{83} - M_{DC}) / RGR \tag{8}$$

At low rust intensities, the yield loss was 1.15 kg ha^{-1}.sori-day^{-1}.$leaf^{-1}$ (Table 5). The avoidable loss (L, kg/ha) is calculated at a 85% fungicide efficacy (Table 3):

$$L = 0.85\ (1.15\ S) \tag{9}$$

To evaluate the profitability of a fungicide application, the expected avoidable loss (L) is compared to the expected costs (C, kg/ha) of a spray:

$$C = (F + A) / P + W \tag{10}$$

in which F is the cost of the fungicide (Dfl/ha), A is the cost for labour and machinery (Dfl/ha), P is the wheat price (Dfl/kg) and W is wheel track damage in kg/ha. At the price level of 1989: F = 70 Dfl/ha, A = 20 Dfl/ha, P = 0.39 Dfl/kg, and W is 0.5% of the expected yield. Thus C is 270 kg/ha at a yield level of 8000 kg/ha. The model, Equations 6-10, calculates the expected profitability of a fungicide application during the season, based on a brown rust observation.

Economic thresholds. Economic thresholds for brown rust control were calculated for different development stages using equations 6-10. To estimate the effect of the expected yield level on the economic threshold, t_{DC} (Eq. 7) was multiplied by 0.9 and 1.1 to mimic a yield level of 6000 and 10 000 kg/ha, respectively. Thresholds were also calculated at a 1.2 times higher and at a 0.8 times lower relative growth rate (Eq. 7)

Table 7. Calculated economic thresholds for brown rust control in the Netherlands at different development stages. Thresholds are given in number of sori per leaf (M) and in fraction of leaves with rust (I). Thresholds are also given for two other yield levels and two other growth rates, see text.

Yield kg/ha	Costs kg/ha	RGR day^{-1}	M/I	Development stages					
				45	55	61	65	71	73
8000	270	0.163	M	0.03	0.07	0.15	0.25	0.56	1.2
			I	0.02	0.04	0.07	0.09	0.16	0.26
6000	260	0.163	M	0.05	0.12	0.26	0.40	0.84	1.7
			I	0.03	0.06	0.10	0.13	0.21	0.32
10000	280	0.163	M	0.01	0.04	0.09	0.15	0.37	0.84
			I	0.01	0.02	0.05	0.07	0.12	0.21
8000	270	0.196	M	0.01	0.02	0.06	0.10	0.28	0.67
			I	0.01	0.02	0.03	0.05	0.10	0.18
8000	270	0.130	M	0.09	0.20	0.38	0.56	1.1	2.0
			I	0.06	0.08	0.12	0.16	0.25	0.36

to mimic the effect of a very susceptible and a moderately susceptible cultivar, respectively. Calculated economic thresholds are given in Table 7. Thresholds are higher during later development stages and at lower yield levels. Different relative growth rates affect the thresholds strongly.

Discussion

The most important result was that brown rust caused a considerable yield loss in all experiments after artificial infections in May. This contrasts with farmers fields as brown rust intensities and subsequent yield loss were low during 1984-86 in the Netherlands. Over the years 1974-86, a lower rust intensity was only recorded in 1976, while nine years had higher rust intensities than recorded in 1984-86 (Daamen et al., in prep.). This indicates that the occurrence of rust epidemics and yield loss depends mainly on the amount of inoculum available in spring and less on weather in June and July (Chester, 1943). Moreover, it indicates that the cultivars grown in the Netherlands are on average too susceptible to avoid yield loss when they are infected in May. Breeding for resistance against yellow rust has been an effective control strategy in the Netherlands over the past ten years. It seems therefore that the most profitable long term strategy will be to manage brown rust through breeding for resistance while relying on fungicides to avoid severe epidemics in the short term.

The advisory model for brown rust was constructed based on relationships and parameters estimated in field experiments. The advantage of this approach is that such experiments do not require a high level of technology and are directly applicable to commercial fields. A limiting factor in the derived model is that the experiments should be done over longer time periods and at different agroecological conditions (climatological regions, yield levels, etc.). Therefore, it is stressed that the calculated thresholds are relevant only for the Netherlands, where susceptible cultivars are grown at a yield level of about 8000 kg/ha and brown rust epidemics usually start after heading. During 1974-86, on average 48% of the commercial fields were infected with brown rust in July (range: 14-92%, Daamen et al., in prep.). Thus monitoring of brown rust is necessary to avoid calendar spraying and to develop integrated control. Wheat crops need to be monitored fortnightly, or, three weeks after a fungicide application. The model was implemented in the computer-based advisory system after 1984, and annually updated with the results of the experiments of 1985 and 1986.

Before resistant cultivars become available, the advisory model leads to a more optimal use of fungicides by avoiding calendar sprays. However, it is clear that the advisory model can be improved. For example, the relative growth rate of brown rust, which was critical to the determination of the thresholds (Table 7), varied considerably but not consistently with year, cultivar and development stage. In Louisiana, growth rates of brown rust could be stabilized over years by cumputing the amount of cumulative degree days above 20 °C (Subba Rao et al., 1990). Here no significant year effect was observed, but the epidemiology of brown rust was not studied in detail. A better understanding of the factors which determine the growth rate of rust in commercial fields is needed to improve brown rust forecasts.

Also other elements of the advisory model, e.g., the precision of monitoring, have a stochastic nature which has not yet been considered. Uncertainties in the advisory model and their consequences at different control tactics are being evaluated (Rossing et al., in prep.).

Acknowledgements

Thanks are expressed to Mr G. van der Vliet and Mr W.J. van den Brink for conducting the experiments and for editing the figures, respectively.

References

Bajwa, M.A., Aqil Khan, A., Khan, N.I. & Arshad Khan, M., 1986. Effect of leaf rust on grain yield and kernel weight of spring wheat. Rachis 5: 25-28.

Buchenau, G.W., 1975. Relationship between yield loss and area under the wheat stem rust and leaf rust progress curves. Phytopathology 65: 1317-1318.

Burleigh, J.R., Roelfs, A.P. & Eversmeyer, M.G., 1972. Estimating damage caused by *Puccinia recondita* f.sp. *tritici*. Phytopathology 62: 944-946.

Chester, K.S., 1943. The decisive influence of late winter weather on leaf rust epiphytotics. Plant Disease Reporter, Supplement 143: 133-144.

Daamen, R.A., 1989. Assessment of the profile of powdery mildew and its damage function at low disease intensities in field experiments with winter wheat. Netherlands Journal of Plant Pathology 95:85-105.

Daamen, R.A., Stubbs, R.W. & Stol, W. (in prep.). Surveys of cereal diseases and pests in the Netherlands. 4. Occurrence of powdery mildew and rusts in winter wheat fields. Netherlands Journal of Plant Pathology.

James, W.C., & Shih, C.S., 1973. Relationship between incidence and severity of powdery mildew and leaf rust on winter wheat. Phytopathology 63: 183-187.

Madden, L.V., Pennypacker, S.P., Antle, C.E. & Kingsolver, C.H., 1981. A loss model for crops. Phytopathology 71: 685-689.

Nachman, G., 1981. A mathematical model of the functional relationship between density and spatial distribution of a population. Journal of Animal Ecology 50: 453-460.

Reinink, K., Jorritsma, I. & Darwinkel, A., 1986. Adaptation of the AFRC phenology model for Dutch conditions. Netherlands Journal of Agricultural Science 34: 1-13.

Rijsdijk, F.H., 1983. The EPIPRE system. Pages 65-76. In: R.B. Austin (Ed.), Decision making in the practice of crop protection. Proceedings 1982 British crop protection symposium. Monograph no. 25. BCPC Publications, Croydon.

Rijsdijk, F.H., Zadoks, J.C. & Rabbinge, R., 1989. Decision making and data management. Pages 265-277. In: R. Rabbinge, S.A. Ward and H.H. van Laar (Eds), Simulation and systems management in crop protection. Pudoc Wageningen.

Seck, M., Roelfs, A.P. & Teng, P.S., 1988. Effect of leaf rust (*Puccinia recondita tritici*) on yield of four isogenic wheat lines. Crop Protection 7: 39-42.

Spitters, C.J.T., Roermund, H.J.W. van, Nassau, H.G.M.G. van, Schepers, J. & Mesdag, J., 1990. Genetic variation in partial resistance to leaf rust in winter wheat: disease progress, foliage senescence and yield reduction. Netherlands Journal of Plant Pathology 96: 3-15.

Subba Rao, K.V., Snow, J.P. & Berggren, G.T., 1989. Effect of growth stage and initial inoculum level on leaf rust development and yield loss caused by *Puccinia recondita* f.sp. *tritici*. Journal of Phytopathology 127: 200-210.

Subba Rao, K.V., Bergren, G.T. & Snow, J.P., 1990. Characterization of wheat leaf rust epidemics in Louisiana. Phytopathology 80: 402-410.

Taylor, L.R., 1961. Aggregation, variance and the mean. Nature (London) 189: 732-735.

Wellings, C.R., Wong, P.T.W. & Murray, G.W., 1985. Use of multiple regression to examine the effect of leaf rust and yellow spot on yield of wheat in New South Wales. Australasian Plant Pathology 14: 62-64.

Zadoks, J.C., 1966. Field races of brown rust of wheat. Proceedings of the cereal rust conferences, Cambridge 1964, PBI, Cambridge, 92-93.

Zadoks, J.C., Chang, T.T. & Konzak, C.F., 1974. A decimal code for the growth stages of cereals. Bulletin Eucarpia 7: 42-52.