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Growth of leek rust epidemics in time in three cultivars during the early stage of the epidemic

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Abstract

The growth of leek rust epidemics in time under favourable conditions in three leek cultivars during two years was analysed. In both years, the highest disease levels were found on cultivar Albana, followed by Carina and Cortina. A simple model is presented to correct the results for exchange of inoculum between adjacent plots. The results of this model indicate, that the difference in rust infection between the cultivars may be due to a reduced growth of the epidemic in young plants of cultivars Cortina and Carina. In older plants, the ranking in susceptibility was reversed, causing a less pronounced difference in infection between the cultivars. The growth of leek rust epidemics during the early stage of the epidemic in isolated plots was satisfactorily described by an exponential model.

Introduction

Rust of leek, caused by *Puccinia allii* Rudolphi, is an important disease of leek (*Allium porrum* L.) in the Netherlands. *P. allii* is a macrocyclic, autoecious rust [Laundon and Waterston, 1966]. In the Netherlands, only the uredo stage plays a role in the epidemiology of leek rust. Sometimes, a few teleutosori can be observed in heavily infected leek crops after a period of warm weather during summer. Aecidia have not been found in the Netherlands.

In the Netherlands, leek cultivation is continuous over the year, with ample overlap between the different crops. The early summer crops are planted in April and harvested in July. The so called late winter crops are planted in July and harvested in May the next year. The uredo stage of leek rust is found around the year in leek crops. In autumn and winter, the growth in the number of uredosori is stopped due to low temperature. As soon as temperature increases during spring, the epidemic of leek rust will start again in late winter crops, causing damage to the crop and providing inoculum to newly planted crops.

There is a large number of leek cultivars, often grouped according to the cropping period. Each group of cultivars has specific characteristics, such as fast growth for early summer cultivars and hardiness for late winter cultivars. Although there is no complete resistance against leek rust at present, differences in susceptibility have been found among cultivars in the United Kingdom [Uma and Taylor, 1991; Smith and Crowther, 1992].

The quality decrease of the product associated with a light infestation of leek rust may cause severe economic loss to the grower. Therefore, chemical control of the disease has to be started in an early stage of the infection. However, applying fungicides to a crop in the absence of the disease is undesirable both from an environmental and an economic point of view. To prevent unnecessary use of pesticides detailed monitoring for presence of the disease is necessary. To assess the presence of the disease in the crop before the disease has increased beyond an intolerable level, frequent sampling is needed and the interval between two samplings should not be taken too long. For the determination of a safe sampling

interval, information on the growth of an epidemic of leek rust in time during the early stage of the epidemic is required.

The aim of this study is to derive a simple predictive model for the early stage of the epidemic to support the development of a sampling method. The growth of leek rust epidemics under favourable conditions in three cultivars during two years was analysed. A simple model was constructed to correct the results for exchange of inoculum between adjacent plots.

Materials and methods

Field observations

Naturally occurring leek rust epidemics were observed in two experiments during summer 1992 and 1993 on a sandy soil nearby Wageningen. In both experiments the same three cultivars were used: Albana, Cortina and Carina. Albana is a fast growing cultivar for harvest in September, Cortina is a cultivar for harvest in late autumn and Carina is a hardy cultivar for spring harvest. In the 1992 experiment, half of the experiment including all three cultivars was planted on 21 May, the other half of the experiment, also including the three cultivars, was planted on 2 July. In the 1993 experiment, there was one planting date: 14 May. For every planting date, the planting material was homogeneous with respect to age and size.

The 1992 experiment consisted of 24 plots, measuring 8 m × 12.5 m. The six combinations of cultivar and planting date were distributed over 4 blocks in a complete randomized block design. The 1993 experiment consisted of 6 isolated plots measuring 10 m × 10 m. The plots were surrounded by a barley crop. The distance between plots was 25 m. The six plots were planted with successively Albana, Cortina and Carina and a repetition of this order. Both experiments were row planted.

The increase of the epidemic was measured by estimating the number of uredosori per plant on randomly selected plants. During the 1992 experiment, the growth of the epidemic was observed weekly from 5 August till 16 September. During this period, there was a considerable difference in growth stage between the two planting dates, as was intended. The plants of the first planting had about two times as much leaves as the plants in the second planting. The epidemic increase in the 1993 experiment was monitored weekly from 28 July till 1 September. In the 1992 experiment, 24 plants per plot were observed. In the 1993 experiment, 1000 plants per plot were observed on 28 July, 4 August and 11 August, 200 plants per plot on 18 August and 100 plants per plot on 25 August and 1 September. The higher number of plants observed in the 1993 experiment was necessary due to the very low percentage of infected plants at the begin of the observations. Details on the experiments are given in Table 1.

Table 1. Details on the 1992 and the 1993 field experiments

	1992	1993
Between row distance (m)	0.50	0.50
Within row distance (m)	0.16	0.16
Plot size (m × m)	8 × 12.5	10 × 10
total number of plots	24	6
Between plot distance (m)	0	25
Planting date	21–5 2–7	14–5
Cultivars	Albana Cortina Carina	Albana Cortina Carina
Observation period	5–8 – 6–9	28–7 – 1–9
Number of plants observed per plot	24	1000 – 100

Mathematical modeling

Growth of the average number of uredosori per plant in a plot during the early stage of a epidemic of leek rust was assumed to follow and exponential model:

$$X(t)_i = X(o)_i e^{r_i t} \quad (1)$$

in which $X(t)_i$ is the mean number of uredosori per plant in plot i at t days after the first observation, $X(o)_i$ is the mean number of uredosori per plant in plot i at the first observation and r_i is the relative growth rate in plot i. Different values of the relative growth rate r_i were assumed for every combination of cultivar and planting date.

In the 1992 experiment, exchange of uredospores between adjacent plots was likely to occur. A simple model was constructed to correct the results for exchange of inoculum between plots. In this model, the number of infections

initiated by autoinfection during one day is assumed to be proportional to the number of uredosori present in the plot, thus assuming exponential growth in absence of alloinfection. Furthermore, it was assumed, that the number of infections initiated in a plot due to alloinfection from an adjacent plot is proportional to the number of infections initiated by autoinfection in that source plot during the same day.

For infections, it takes a period of latency to become uredosori. The latent period was assumed to be constant for all infections (p days). In other words, the number of uredosori occurring during one day in plot i due to autoinfection is proportional to the number of uredosori that was present in the plot p days before that day. The corresponding proportionality factor is the relative multiplication fact R_i and different values were assumed for each combination of cultivar and planting date. The number of uredosori occurring during one day in plot i due to alloinfection from an adjacent plot j is proportional with a factor *disp* to the product of R_j times the number of uredosori that was present in plot j p days before that day.

The mathematical model based on these assumptions is:

$$X(t+1)_i = X(t)_i + R_i * X(t-p)_i + \sum_{j=1}^{n} disp * R_j * X(t-p)_j \quad (2)$$

in which $X(t)_i$ is the mean number of uredosori per plant in plot i at day t, R_i is the relative multiplication factor for plot autoinfection in plot i, *disp* is the proportionality factor for alloinfection from neighbour plot j and n is the number of plots contributing to alloinfection.

The proportionality factor for alloinfection *disp* is assumed to be equal for all adjacent plots, i.e. plots sharing a side or a corner. Furthermore, it is assumed, that between plots that are not adjacent, exchange of uredospores is negligible. Model (2) only holds, when size and planting density are equal for all plots.

The following relation was used to calculate the relative growth rate r from the relative multiplication factor R:

$$R = (e^r - 1) * e^{rp} \quad (3)$$

Formula (3) follows from the requirement, that model (1) and (2) must be identical after omission of the term for alloinfection from model (2) (see the appendix).

Parameter estimation

A general procedure in non-linear curve fitting to obtain estimates of parameters (Θ) in the model, is minimizing the sum of squares of the residuals:

$$\sum_{j=1}^{m} (y_j - f(X_j, \Theta))^2 \quad (4)$$

in which y_j is an observation, $f(x_j, \Theta)$ the corresponding value of the model and m is the total number of observations, i.e. the product of the number of plots times the number of observation days [Richer and Söndgerath, 1990]. In minimizing (4), all observations are weighted equally, which is a natural procedure, when the variance of the observations is the same for all observations (homogeneity of variance). However, with population growth, often an increase of the variance of the observations is found with time. A logarithmic transformation of the observations can sometimes be useful to remove the inhomogeneity of variances [Doucet and Sloep, 1992]. The corresponding estimation of Θ is obtained by minimizing the sum of squares of the residuals of the logarithmic transformed values:

$$\sum_{j=1}^{m} (\ln(y_j) - \ln(f(X_j, \Theta))^2 \quad (5)$$

A more general procedure to obtain these so called least square estimates of parameters (Θ) for observations with a complicated error structure, is minimizing the sum of squares of the residuals weighted for the variance in the individual observations:

$$\sum_{j=1}^{m} \frac{1}{\sigma_j^2} (y_j - f(X_j, \Theta))^2 \quad (6)$$

in which σ_j^2 is the variance of an observation. Usually, σ_j^2 will be unknown and replaced by estimated variances. In this study, variances are estimated by taking the measured variance in the observations. Without further assumptions, this method of estimation, known as weighted least

squares, has only an intuitive appeal, but under certain distributional assumptions regarding y_j a widely accepted justification is found in likelihood theory [Richter and Söndgerath, 1990].

The approximate minimum of (4), (5) and (6) for models (1) and (2) was found numerically with the down hill simplex algorithm [Press et al., 1986]. The initial value for the mean number of uredosori per plant in a plot $X(o)_i$ was estimated as a parameter with a positive value, that was restricted to be within the 95 % confidence limits of the observed initial mean number of uredosori per plant in that plot. For the 1992 experiment, (Θ) consisted of 24 initial values $X(o)_i$ and r values for each of the six combinations of cultivar and planting date. For model (2), the parameter *disp* was estimated in addition. For the 1993 experiment, (Θ) consisted of six initial values $X(o)_i$ and three cultivar dependent r values. For both experiments, an alternative (Θ) having only one pooled r value was estimated. The parameter estimation was performed by using the observations from all plots in an experiment simultaneously. The length of the latent period (p) in model (2) was not estimated as a parameter, but considered as a constant. The value of this constant p was taken as the shortest period between infection and occurrence of sporulating uredosori as observed in various experiments with artificial inoculation during 1991, 1992 and 1993. Model (2) was initialized for $-p \leq t < 0$ by neglecting alloinfection over this period and backward calculation of $X(t)_i$ with model (1) starting from $X(o)_i$.

As a measure for goodness of fit, a non-linear coefficient of determination (R^2) is used, defined as:

$$R^2 = 1 - \frac{\sum_{j=1}^{m} (y_j - f(X_j, \hat{\Theta}))^2}{\sum_{j=1}^{m} (y_j - \overline{y})^2} \qquad (7)$$

in which ($\hat{\Theta}$) is the set of estimated values for (Θ).

Results

In the 1992 experiment, the first planting was already infected when the second planting was planted. Therefore, the disease levels in the first planting were higher than in the second planting. In both plantings, highest disease levels were found on cultivar Albana, followed by Carina and Cortina. The same ranking was found in the 1993 experiment. In the 1993 experiment, the epidemic started later and consequently, the disease level during the observation period was lower than in the 1992 experiment. The mean pustule number per plant at the first and last date of observation are given in Table 2 for the 1992 experiment and in Table 3 for the 1993 experiment.

In both years, there was a strong dependence of the variance in the observations on the level of the observed mean number of uredosori per plant (Fig. 1 and Fig. 2), a commonly described phenomenon [Daamen, 1986]. This inhomogeneity of variance can be explained by several factors. First, some plants only have very low pustule numbers, even at high levels of disease infection, thus causing the variance in the observed mean pustule number to increase with increasing disease levels. Secondly, at increasing numbers of uredosori per plant, the estimation of the number of uredosori per plant became more inaccurate. It was more easy to distinguish between 20 and 50 uredorori per leaf than between 200 and 500 uredosori per leaf. Furthermore, in the 1993 experiment, the number of plants observed per plot decreased with increasing disease level.

Given the strong dependence of the variance in the observations on the level of the observation,

Table 2. Mean uredosori number per plant in the 1992 experiment at the begin and the end of the observation period; values are the averages per combination of cultivar and planting date over the four blocks; values with the same letter are not significantly different (ANOVA on plot means, $\alpha = 0.05$)

Date	Planted on 21–5			Planted on 2–7		
	Albana	Cortina	Carina	Albana	Cortina	Carina
5–8	65.6a	4.2b	19.7c	0.7b	0.2b	0.8b
16–9	1637a	559b	837c	337bd	88d	165d

Table 3. Mean uredosori number per plant in the 1993 experiment at the begin and the end of the observation period; values are the averages per cultivar; values with the same letter are not significantly different (ANOVA on plot means, $\alpha = 0.05$)

Date	Albana	Cortina	Carina
28–7	0.34a	0.08a	0.18a
1–9	58.0a	21.2b	41.3ab

the weighted sum of squares (6) is more likely to produce reliable estimates for the model parameters from a theoretical point of view. However, since this method of parameter estimation is not always possible, e.g. due to lack of information on the variance in the observations, the results of the other two estimation methods are given as well for comparison.

The length of the latent period (p) in model (2)

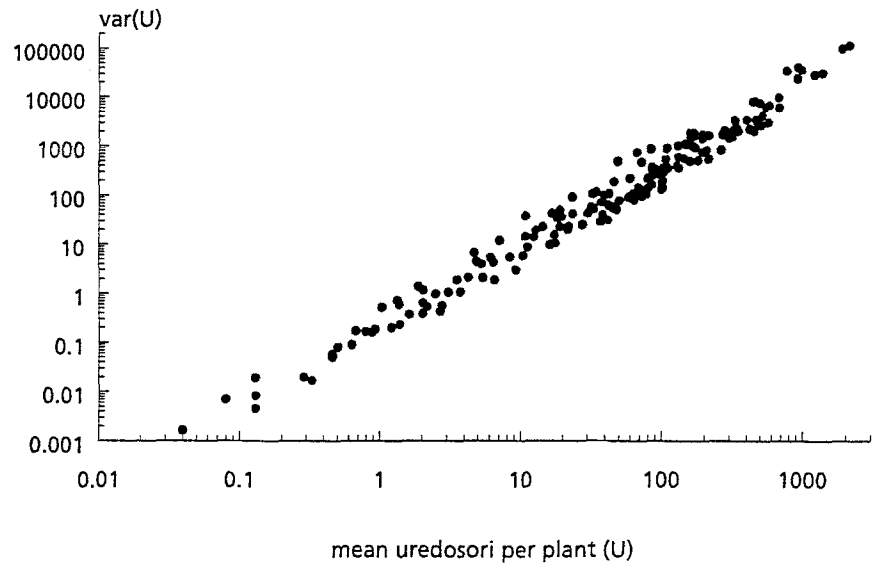

Fig. 1. Relation between sample variance in the observations and the level of observed mean number of uredosori per plant for the 1992 experiment.

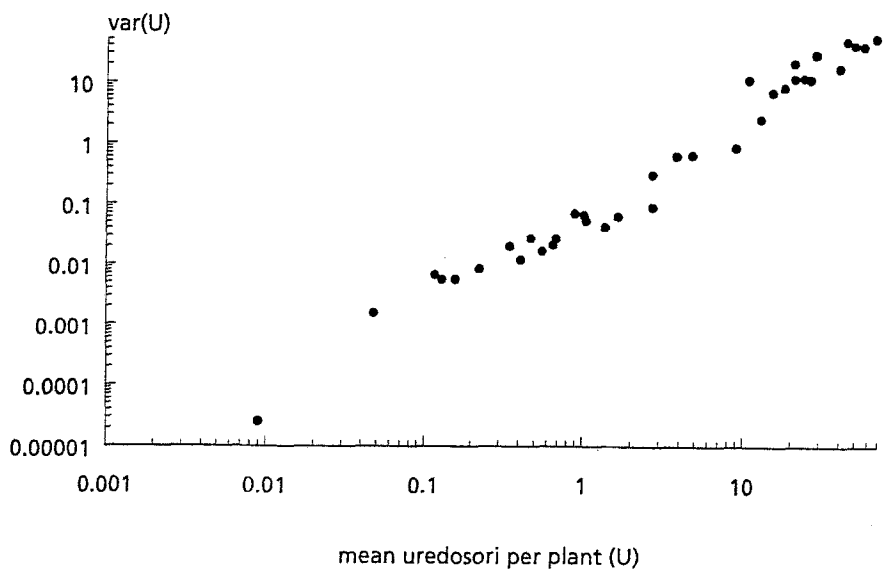

Fig. 2. Relation between sample variance in the observations and the level of observed mean number of uredosori per plant for the 1993 experiment.

was taken as 12 days. This was the shortest period between inoculation and occurrence of sporulating uredosori as observed during August and September 1991 in inoculated leek plants (cv. Jolant), that were transferred to the experimental site. In greenhouse experiments, the latent period was equal for the cultivars Albana, Cortina and Carina, although somewhat longer than for cultivar Jolant under field conditions (Table 4).

The values for the relative growth rates as estimated with the two models and the three methods for parameter estimation are given in Table 5 for the 1992 experiment and in Table 6 for the 1993 experiment. As plots were isolated in the 1993 experiment, only the simple exponential model (1) was applied. In general, good fit was obtained with both models, except when the logarithmic transformation (5) was used for parameter estimation.

Estimation of the relative growth rates with the simple exponential model (1), gave no clue on the difference in infection observed in the 1992 experiment. The estimated relative growth rate was lowest for Albana as compared to Cortina and Carina in both planting (Table 5), whereas the observed disease levels were highest (Table 2). However, the results of the dispersion model (2) indicated, that the high values for the relative growth rate in the second planting as estimated with the simple exponential model (1) can be explained by influx of inoculum from the severely infected plots of the first planting (Fig. 3). The dispersion model (2) produced estimates for the relative growth rate for the second planting of cultivars Cortina and Carina in absence of alloinfection, that were lower than the estimates obtained with the simple exponential model (1). These results suggest, that the difference in rust infection between the cultivars was due to a reduced growth of the disease in young plants of cultivars Cortina and Carina. In older plants, the ranking in susceptibility was reversed, causing the difference in infection between the cultivars to become less pronounced.

For the 1993 experiment, the simple exponential model (1) resulted in a good fit with the observed uredosori numbers (Fig. 4). The same ranking in the estimates for the relative growth rate was found as for the first planting of the 1992 experiment, that had about the same age during observation (Tables 5, 6). In both cases, cultivar Cortina had the highest relative growth rate, followed by Carina and Albana. Only method (4) for parameter estimation resulted in a higher relative growth rate for Albana than the one for Carina in the 1993 experiment. The estimated values for the relative growth rate for the three varieties in the 1993 experiment were higher than

Table 4. The latent period (p), i.e. the shortest period between artificial inoculation and the occurrence of sporulating uredosori as observed in various experiments and details on these experiments

Year	Date of inoculation	Location of inoculated plants (*)	Cultivar	Age of plants (months)	Number of Plants	p (days)
1991	1–8	1	Jolant	2	40	12
	8–8	1	Jolant	2	40	10
	14–8	1	Jolant	2	40	11
	21–8	1	Jolant	2	40	11
	28–8	1	Jolant	2	40	12
	4–9	1	Jolant	2	40	12
	11–9	1	Jolant	2	40	12
	18–9	1	Jolant	2	40	12
1992	10–7	2	Jolant	5	144	12
1993	15–4	2	Albana	8	39	14
	15–4	2	Cortina	8	47	14
	15–4	2	Carina	8	47	14
	18–6	3	Albana	4	45	14
	18–6	3	Cortina	4	45	14
	18–6	3	Carina	4	45	14

(*) 1. experimental site (same as for 1992 and 1993 field experiments), 2. under plastic tunnel at institute, 3. greenhouse 20 °C.

Table 5. Relative growth rates for the different combinations of cultivar and plant age as estimated from the 1992 experiment and the corresponding value for the non-linear coefficient of determination (R^2); for model (2) also the estimate for the proportionality factor for alloinfection (*disp*) is given

Model (*)	Parameter estimation method (*)	Relative growth rate (d^{-1})						*disp*	R^2
		Pooled	Planted on 21–5			Planted on 2–7			
			Albana	Cortina	Carina	Albana	Cortina	Carina	
1	4	0.09							0.72
1	5	0.10							0.04
1	6	0.09							0.69
1	4		0.08	0.12	0.10	0.14	0.15	0.17	0.94
1	5		0.08	0.12	0.10	0.15	0.17	0.19	0.84
1	6		0.07	0.12	0.09	0.14	0.15	0.18	0.84
2	4	0.08						0.04	0.91
2	5	0.09						0.04	0.86
2	6	0.08						0.04	0.87
2	4		0.08	0.13	0.11	0.13	0.08	0.12	0.02	0.95
2	5		0.08	0.10	0.09	0.11	0	0.09	0.04	0.88
2	6		0.07	0.10	0.09	0.12	0.05	0.11	0.03	0.85

(*) numbers refer to the numbers of the formulae in the text.

Table 6. Relative growth rates for the different cultivars as estimated from the 1993 experiment and the corresponding value for the non-linear coefficient of determination (R^2)

Model (*)	Parameter estimation method (*)	Relative growth rate (d^{-1})				R^2
		Pooled	Albana	Cortina	Carina	
1	4	0.16				0.85
1	5	0.18				0.22
1	6	0.16				0.83
1	4		0.15	0.20	0.14	0.89
1	5		0.16	0.20	0.17	0.39
1	6		0.15	0.20	0.16	0.85

(*) numbers refer to the numbers of the formulae in the text.

those for the first planting of the 1992 experiment (Tables 5, 6).

Due to the late start of the epidemic in the 1993 experiment, no observations could be done on the epidemic growth in the young crop. However, the initially observed disease levels suggest, that the susceptibility of the three cultivars in young plants was in a reversed order compared to the susceptibility in older plants (Table 2).

The methods of parameter estimation (4) and (5) produced values for the relative growth rate comparable to those obtained with the theoretically more attractive method (6). However, in some cases the differences were considerable. One example is the zero value for the relative growth rate in the second planting of cultivar Contina as estimated with model (2) and parameter estimation method (5), that falsely suggests complete resistance in young plants of cultivar Cortina. The ranking in relative growth rates between the varieties and planting dates in the 1992 experiment did not depend on the method of estimation. In the 1993 experiment, method (4) produced a different order from the other two methods.

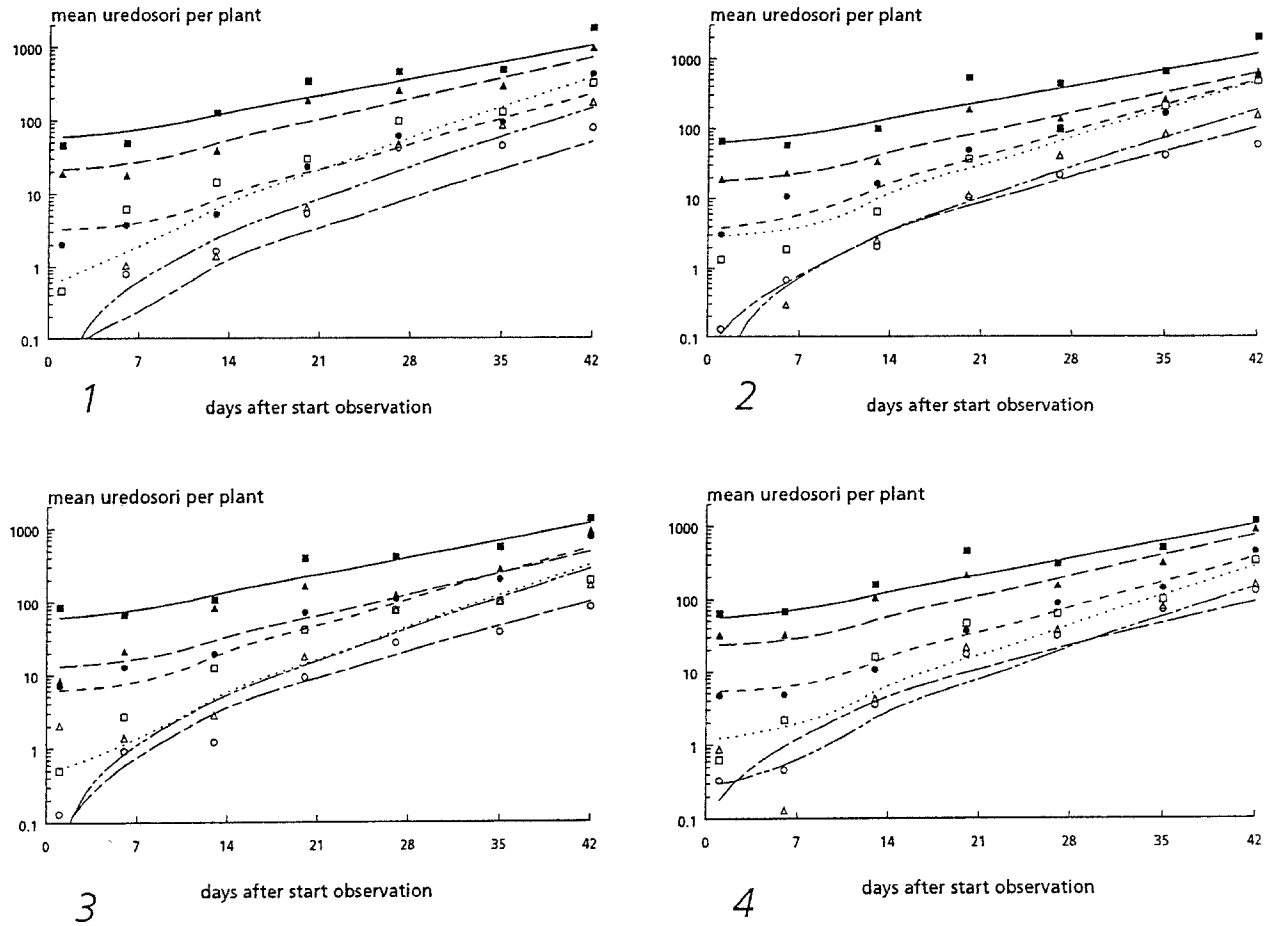

Fig . 3. Observed (markers) and simulated (lines) leek rust epidemics in the individual plots for the 1992 experiment; the dispersion model (2) was used together with method (6) for parameter estimation; first planting: (■, ——) Albana, (▲, ——) Carina, (●, – – –) Cortina; second planting: (□, - - - -) Albana, (△, — - - —) Carina, (○, — - —) Cortina; the numbers under the graphs refer to the block number.

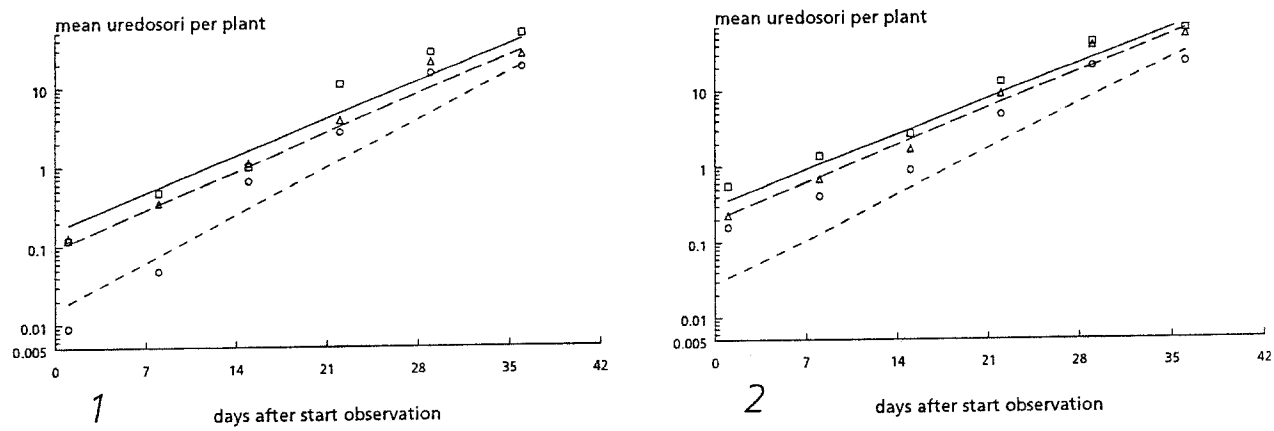

Fig. 4. Observed (markers) and simulated (lines) leek rust epidemics in the individual plots for the 1993 experiment; the exponential model (1) was used together with method (6) for parameter estimation; (□, ——) Albana, (△, ——) Carina, (○, – – –) Cortina; 1. the three western plots, 2. the three eastern plots.

Discussion

The dispersion model (2) was kept as simple as possible to reduce the number of parameters as much as possible. In fact, only one parameter was used to characterize transport of spores between plots and this parameter was estimated from the disease observations simultaneously with the relative growth rates. The price paid for this simplification was that several assumptions had to be made. The transport of spores between plots was assumed to be symmetrical and constant over the observation period and to occur only between neighbouring plots. Another simplification was, that the length of the latent period was taken identical for all infections, irrespective of the combination of cultivar and planting date. This simplification is partly justified by the observations and the findings of Jennings et al. [1990].

A more detailed model for exchange of inoculum between plots was given by Paysour and Fry [1983]. The dispersion model (2) in this study is more suited to correct experimental results for exchange of inoculum between adjacent plots than the more detailed model of Paysour and Fry [1983], but it is less useful for theoretical studies on the effect of plot size and distance. In the dispersion model (2), the value for the parameter for alloinfection is specific for a particular experimental layout and dispersal conditions and this value can not be extrapolated to other experimental layouts or dispersal conditions.

The highest values for the non-linear coefficient of determination (7) are always obtained, when the simple method (4) for parameter estimation is used. This is not surprising, as method (4) is in fact maximization of the non-linear coefficient of determination (7). The sometimes poor fit obtained with the logarithmic transformation (5) is a general drawback of this method [Doucet and Sloep, 1992]. In botanical epidemiology, the logarithmic transformation is often used to transform the exponential growth function in a linear function, in order to apply linear regression techniques. However, in applying the logarithmic transformation and subsequent linear regression, the thus estimated parameters not necessarily produce an optimal fit of the exponential model to the non-transformed date.

The results of both experiments show, that the growth of an epidemic of leek rust is dependent on the age of the crop. Jennings et al. [1990] found a decrease in susceptibility with increasing plant age in the leek cultivar Musselburgh. The results from the present study also indicate, that the effect of plant age is differing from cultivar to cultivar. In cultivar Albana, susceptibility was higher in younger plants than in older plants, whereas in cultivar Cortina it was the other way round. The inconsistency in the ranking of the susceptibility for leek rust among several leek cultivars at different observation dates as found by Smith and Crowther [1992], can be explained by assuming a similar interaction between cultivar and the effect of crop age on susceptibility.

Both experiments showed a consistent effect of cultivar and plant age on the growth of the leek rust epidemic. However, from the differences in the relative growth rates as estimated for the 1992 and the 1993 experiment, it is clear, that other factors than cultivar and plant age can have an effect on the growth of the leek rust epidemic. Although it is beyond the scope of this study to identify the exact causes of these differences, weather conditions and growing conditions of the leek crop can be mentioned as possible ones.

The growth of leek rust epidemics during the early stage of the epidemic in isolated plots was satisfactorily described by an exponential model. For predictive purposes, the value for the relative growth rate should be chosen with some care, as this parameter was found to be variable, depending among other factors on cultivar and plant age. The consequences of the variability of the relative growth rate for the determination of a safe sampling interval will be discussed in a subsequent paper.

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Appendix

A discrete version of model (1) is

$$X_t = X_0(1 + r_d)^t \quad (8)$$

with difference equation:

$$X_{t+1} = (1 + r_d)X_t \quad (9)$$

in which r_d is the growth rate for discrete time steps (days). Formula (9) can be rewritten as

$$X_{t+1} - X_t = r_d X_{t-p}(1 + r_d)^p \quad (10)$$

in which p is the latent period in days. Omitting the term for alloinfection from model (2) yields:

$$X_{t+1} - X_t = RX_{t-p} \quad (11)$$

Combination of equation (10) and (11) gives:

$$R = r_d(1 + r_d)^p \quad (12)$$

From (1) and (8) it follows that:

$$r_d = e^r - 1 \quad (13)$$

Substituting r_d by r in (12) gives:

$$R = (e^r - 1) * e^{rp} \quad (3)$$

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