European Journal of Plant Pathology **101**: 431–439, 1995.

Life-table analysis of faba bean rust

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Accepted 19 January 1995

Key words: comparative epidemiology, infection efficiency, monocyclic analysis, sporulation rate, *Uromyces viciae-fabae, Vicia faba*

Abstract

In controlled near-optimum conditions (18 °C), monocyclic sporulation capacity and spore infection efficiency were assessed for faba bean rust on the first and second leaves of field bean. After a latency period of 8–10 days, lesions sporulated during *c.* 50 days. Spore production on the second leaf, *c.* 9×10^4 spores per lesion, was two times as high as spore production on the first leaf. Infection efficiency was similar for both leaf layers, with a mean value of 0.11 lesion per inoculated spore. Infection efficiency decreased strongly when spores originated from mother lesions older than 20 days. Three life-table statistics (the net reproduction number R_o, the mean generation time T_g, and the maximum relative growth rate r_{max}) were calculated. R_o was larger and T_g was longer for the second than for the first leaf, but r_{max} was nearly the same for both leaf layers (0.31–0.33 day^{-1}). r_{max} was compared with the exponential growth rate r measured in a field experiment. From the difference between the two rates, the fraction of inoculum lost in field conditions was estimated at 0.54–0.94. The life-table statistics were also compared to those of other legume rusts, and implications of life-table analysis for comparative epidemiology were discussed.

Introduction

Growth-chamber experiments have been widely used to assess epidemic components in rust fungi [Mehta and Zadoks, 1970; Teng and Close, 1978; Sache and de Vallavieille-Pope, 1993]. Monocyclic components of disease such as latent period, infectious period, spore production, and infection efficiency were used to characterize fungal life strategies [Zadoks and Schein, 1979; Sache and de Vallavieille-Pope, 1993], to evaluate partial resistance components of cultivars [Zadoks, 1972; Parlevliet, 1979; Leonard and Mundt, 1984], or as input values for disease simulation models [Zadoks, 1971].

The effect of monocyclic parameters on the polycyclic progress of disease is difficult to assess in field experiments due to the many of interacting biotic and abiotic factors. Simulation of disease progress using monocyclic parameters and avoiding the complexity of the outdoor situation led to a better understanding of fungal population dynamics. Results obtained in optimum situations [Leonard and Mundt, 1984; Sache and de Vallavieille-Pope, 1993] may be used as a reference for further work dealing with more complex disease situations.

Life-table analysis received much attention from animal and plant ecologists [Begon *et al.*, 1986], because it translates many measured biological variables into a few demographic parameters which fully characterize the dynamics of the population. Application of life-table analysis to pathogenic fungi was reported only in the case of

brown (leaf) rust of wheat (*Puccinia recondita* f. sp. *tritici*), where it proved to be an efficient tool to link monocyclic and polycyclic processes without designing large-scale experiments [Zadoks, 1977]. Life-table analysis may also contribute to understand the disease dynamics of faba bean rust (*Uromyces viciae-fabae*).

As no quantitative information about monocyclic parameters for this rust is available in the literature, the objective of the work reported here was to build a life-table for faba bean rust. Growth-chamber experiments were designed to quantify the monocyclic parameters of disease in conditions highly conducive to disease. The theoretical rate of disease increase, obtained from life-table analysis, was finally compared with the rate of increase of disease measured in a field experiment with the same combination of bean cultivar and rust isolate.

Materials and methods

Spore production

Faba beans (*Vicia faba*) cv. Alfred (Cebeco Zaden BV, Rotterdam, The Netherlands), highly susceptible to rust, were sown in 11-cm plastic pots. Plants were grown in a growth chamber at 20 °C with a 16-h day photoperiod. Six incandescent tubes (Philips 40W133 RS) provided *c.* 13 $W.m^{-2}$ (9000 lux) at the first leaf level. Plants were thinned after emergence to three stems per pot. Ten-day old plants, with two leaves fully unfolded, were placed on the bottom of a settling tower. Two mg of urediniospores (hereunder called spores) were forcibly dispersed upwards in the tower by discharge of a carbon dioxide pistol and were allowed to settle onto the leaves during 5 min. Inoculated plants were incubated for 24h at 18 °C in a water-saturated atmosphere and kept at 18 °C with a 16-h day photoperiod and a light intensity of 13 $W.m^{-2}$. Plants were tied to vertical wooden stakes to maintain the leaves in a horizontal position and minimize passive spore loss. Stipules and upper leaves were cut away when bearing sporulating lesions.

Beginning two days after the beginning of sporulation, spores were collected separately from the first and second leaves with a miniaturized cyclone collector connected to a vacuum pump [Mehta and Zadoks, 1971]. Each replication included 1–3 leaves with an average pustule density of 10.0 $pustules.cm^{-2}$ (7 replications) for the first leaves, and 8.4 $pustules.cm^{-2}$ (5 replications) for the second leaves. Spores were collected every two or three days to allow the lesions to recover from mechanical disturbance caused by the collection procedure. Passive loss of spores between collection dates was minimized by laying pieces of greaseproof paper on the pot surface under the sporulating leaves. Immediately after collection from the leaves and the greaseproof paper pieces, spores were weighed in the collecting vial, of which the unloaded weight had been determined previously. Preliminary experiments with a Coulter Counter® (Coultronics SA, Margency, France) showed that 1 mg of freshly collected spores yielded about 170,000 uredospores, and spore weights were transformed to spore numbers using this relationship.

Since the time between successive collection dates was not constant over the whole experiment, the sporulation rate (r_S) was not directly evaluated from the number of spores collected at each date (x_t, with t in days after inoculation). The accumulated spore production (y_n) between the beginning of sporulation (t_o) and the n^{th} observation date was calculated as:

$$y_n = \sum_{i=o}^{i=n} x_i \qquad (1)$$

The sporulation rate was evaluated for each date using a three-point differentiation formula [Jeger, 1980]:

$$r_S(t) = [h_1^2 * y_{n+1} + (h_2^2 - h_1^2) * y_n - h_2^2 * y_{n-1}]/[h_1 * h_2 * (h_1 + h_2)] \qquad (2)$$

where

h_1 = time between the $(n - 1)^{th}$ and the n^{th} observation dates

h_2 = time between the n^{th} and the $(n + 1)^{th}$ observation dates

Equation (2) produces an estimation of the rate r_S centered at each date and not between dates. A detailed justification of use of equation (2) rather than linear interpolation of the rate between pairs of successive dates is given in Campbell and Madden [1990, pp. 155–157].

Infection efficiency

Spores produced during two- or three-day periods were collected as previously described. Aliquots of 1–2 mg of these spores were used as inoculum in the settling tower. Inoculation of 1 mg of spores resulted in a deposited spore density of 100 spores.cm^{-2}. The density and the uniformity of spore deposit were regularly checked using glass slides. Ten days after inoculation, the number of sporulating lesions was counted, the leaf area was measured with a LI-3100 Area Meter (Li-Cor, Inc., Lincoln, USA), and infection efficiency was calculated as the ratio of the number of sporulating lesions.cm^{-2} to the number of deposited spores.cm^{-2} [Schein, 1964].

Latent and infectious periods

Latent and infectious periods were quantified in a separate experiment without mechanical disturbance. Plants were inoculated and further grown as described before. The number of non-sporulating, sporulating and dead lesions was counted daily.

Statistical analyses

The effects of leaf layer and observation date and of the interaction leaf layer × observation date on the sporulation rate, the infection efficiency, and the latent period were studied using analysis of variance with repeated measures. Data for infection efficiency and latent period were submitted to angular transformation before analysis. Calculations were performed with StatView® (Abacus Concepts, Berkeley, USA).

Life-table analysis

A fertility table [Zadoks, 1977] was built using the results of these two experiments. The age-specific reproductive rate $m(t)$ was defined as the potential number of daughter lesions produced per mother lesion during the period ending at time t. $m(t)$ was calculated as the product $r_S(t) * IE(t)$, where $IE(t)$ is the infection efficiency of the spores produced during the period ending at time. The survivorship rate, i.e. the relative survival frequency at age t, $l(t)$, was defined as the normalized proportion of sporulating lesions As the initial number of infections could not be known, the maximum number of sporulating lesions observed during each experiment was set at 1.

Three statistics usually computed from life-tables [Begon *et al.*, 1986] were slightly transformed to have epidemiological significance [Zadoks and Schein, 1979], as follows:

– The net reproduction number (R_o), or progeny/parent ratio, is the potential number of daughter lesions produced by a mother lesion during her whole life (here from t_o to t_n, the last date of calculation of the sporulation rate). R_o was calculated as:

$$R_o = \sum_{t=t_o}^{t=t_n} l(t) * m(t) \qquad (3)$$

– The mean generation time (T_g), expressed in days is an approximation of the duration of each cycle in a polycyclic epidemic. T_g was calculated as:

$$T_g = \sum_{t=t_o}^{t=t_n} t * l(t) * m(t)/R_o \qquad (4)$$

– The maximum relative growth rate r_{max}, expressed in number of daughter lesions per mother lesion per day, sets an upper limit to the rate of population development when all parameters are measured under optimum conditions. r_{max} is approximatively related to R_o and T_g by:

$$r_{max} = \ln(R_o)/T_g \qquad (5)$$

Using data from the literature, life-tables were built also for rusts on soybean (*Glycine max*), common bean (*Phaseolus vulgaris*), and groundnut (*Arachis hypogaea*).

For soybean rust (*Phakopsora pachyrhizi*), r_S was evaluated from sporulation curves published for two soybean cultivars [Yeh *et al.*, 1982, Fig. 4]. Infection efficiency was kept constant in the calculations, using the maximum value of 0.06 reported by Melching *et al.* [1988]. For common bean rust (*U. appendiculatus*), r_S was evaluated from the sporulation curve published by Imhoff *et al.* [1982, Fig. 2, low density]. Infection efficiency was kept constant in the calculations, using the maximum value of 0.08 reported by Statler and McVey [1987]. For groundnut rust (*Puccinia arachidis*), r_S was evaluated from the sporulation data published by Subrahmanyam *et al.* [1983, Fig. 2B, cv. TMV-2]. Infection efficiency was kept constant in the calculations, using the median

value of 0.24 reported by Savary [1985] for dry inoculation.

In all three cases, no lesion death before the end of experiment was assumed, thus setting $l(t) = 1$ for every t value.

Evaluation of inoculum loss in field conditions

The same faba bean cultivar and the same rust isolate were used to study disease increase and spread in a field experiment [Sache and Zadoks, unpubl.]. Three plants located in the centre of a 16-m^2 plot were inoculated with spores suspended in mineral oil (Soltrol 170, Phillips Chemical Co., Bartlesville, USA), and rust severity was regularly scored on all plants of the plot. Climatic conditions were very conducive to disease, which spread througout the entire plot. In plants located beyond 2 m from the inoculated centre, saturation of host tissue was not reached at the end of the epidemic (59 days after inoculation) and disease increase was exponential. The apparent infection rate (r) for the lower canopy layer was calculated as:

$$r = [\ln(x_n) - \ln(x_o)]/(t_n - t_o) \quad (6)$$

x_n and x_o being the disease severities at the end (t_n) and in the beginning (t_o) of the epidemics, respectively [Van der Plank, 1963]. As climatic conditions were very conducive to disease, the difference between r_{max} and r was mainly attributed to spore loss during dispersal under field conditions. r is related to the life-table statistics and the fraction of inoculum lost in field conditions (ΔS):

$$r = \ln[R_o * (1 - \Delta S)]/T_g \quad (7)$$

After rearranging equation (7) and incorporating equation (5), ΔS was evaluated as:

$$\Delta S = 1 - \exp[-(r_{max} - r) * T_g] \quad (8)$$

Results

Spore production

The sporulation rates for the first and second leaves strongly differed (Fig. 1). Analysis of variance showed significant effects ($P < 0.001$) of leaf layer, time, and time × leaf layer interac-

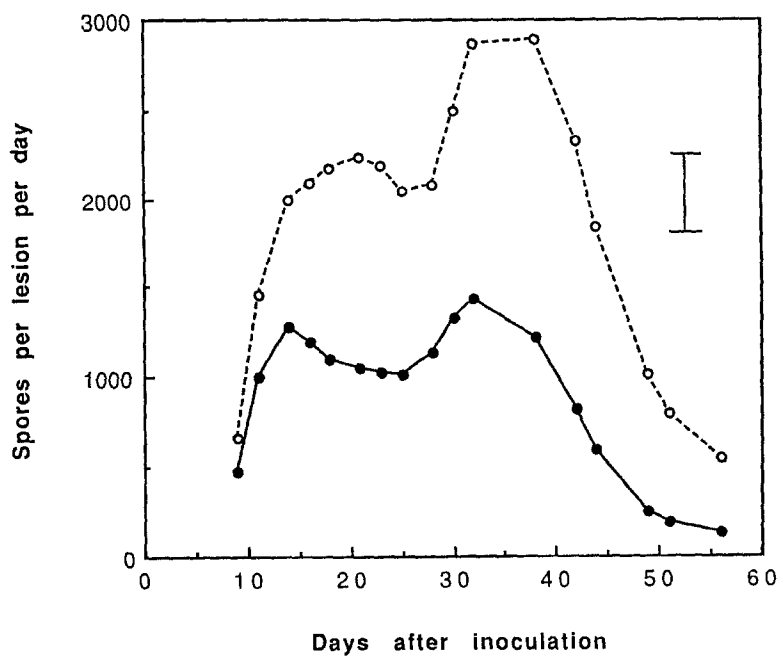

Fig. 1. Sporulation rate in *Uromyces viciae-fabae* on first (closed circles, solid line) and second (open circles, dashed line) leaves of faba bean cv. Alfred. Vertical bar represents the standard error of a difference between two means (SED).

tion on sporulation rate. On the first leaf, the sporulation rate reached a peak 14 days after inoculation, then slightly decreased till 25 days after inoculation. A second peak, slightly higher than the first one, was reached 32 days after inoculation. On the second leaf, the first sporulation peak occurred 21 days after inoculation. The sporulation rate then slightly decreased until 25 days after inoculation. The second peak, 38 days after inoculation, was far more pronounced than for the first leaf, accounting for most of the interaction effect. The sporulation rate decreased monotonically after the second peak on both leaf layers. A few lesions still produced small amounts of spores 65 days after inoculation.

Total spore production per lesion for the second leaf, about $(9.3 \pm 2.5) \times 10^4$ spores per lesion, was more than twice that for the first leaf, about $(4.3 \pm 0.9) \times 10^4$ spores per lesion.

Infection efficiency

The pattern of infection efficiency differed for spores collected from the first and second leaves (Fig. 2). Analysis of variance showed significant effects ($P < 0.001$) of time and time × leaf layer interaction. Leaf layer had no significant effect ($P = 0.49$). Infection efficiency and sporulation rate at different dates showed a strong positive correlation ($r = 0.83$, $P < 0.001$) for the first leaf, implying a strong association between the quantity and the quality of the spores. On the second leaf, the peaks in sporulation rate were associated with either minimum or decreasing infection efficiency, and no significant correlation was found between infection efficiency and sporulation rate.

Latent and infectious periods

On the first leaf, the maximum number of sporulating lesions was reached 10 days after inoculation. 75% and 98% of these lesions sporulated 8 and 9 days after inoculation, respectively. No sporulating lesion was observed 7 days after inoculation and earlier. All lesions were still sporulating 30 days after inoculation. The leaves became heavily damaged by rust later on, and it was impossible to decide whether the lesions were still sporulating or not. Similar results were obtained for the second leaf.

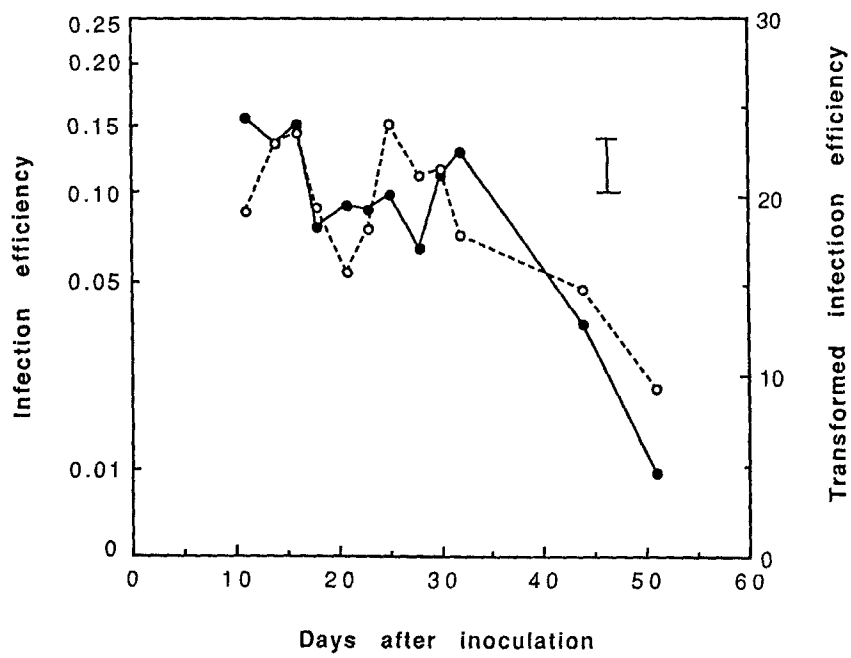

Fig. 2. Infection efficiency versus days after inoculation in *Uromyces viciae-fabae* collected from first (closed circles, solid line) and second (open circles, dashed line) leaves of faba bean cv. Alfred. Each dot represents the mean number of pustules. cm^{-2} relative to the number of applied spores. cm^{-2}, using spores taken from pustules on the indicated day after inoculation. Values (left hand scale) were submitted to angular transformation (right hand scale). The vertical bar represents the standard error of a difference between two transformed means (SED).

Life-table analysis

Because of the lack of information on lesion survivorship, the survivorship $l(t)$ was set at 1 for the whole experiment period. Differences between first and second leaves in the three life-table statistics (Table 1) were largest for R_o. For the second leaf, R_o was 1.9 times the value obtained for the first one. T_g for the second leaf was 1.1 times that for the first one. r_{max} for the second leaf was 0.94 times that for the first one.

Table 1 includes life-table statistics calculated for other legume rusts, assuming no lesion death during the infectious period. The four studied legume rusts ranked differently according to the three life-table statistics. Ranking according to increasing R_o value was:

soybean < faba bean (leaf 1) < groundnut < faba bean (leaf 2) < common bean.

Ranking according to decreasing T_g value was:

soybean > faba bean (leaf 2) > common bean > groundnut > faba bean (leaf 1).

Ranking according to increasing r_{max} value was:

soybean < faba bean < groundnut < common bean.

Table 1. Comparison of life-table statistics[1] R_o, T_g and r_{max} for four legume rusts, assuming no lesion death during the infectious period

Rust	R_o	T_g	r_{max}
Uromyces viciae-fabae (faba bean)[2]			
first leaf	1748	22.9	0.33
second leaf	3273	25.8	0.31
Phakopsora pachyrhizi (soybean)[3]			
cv. TK 5	565	28.2	0.23
line PI 230971	760	27.5	0.24
Puccinia arachidis (groundnut)[4]	2911	23.3	0.34
Uromyces appendiculatus (bean)[5]	12976	24.9	0.38

[1] R_o is the net reproduction rate (daughter lesions per mother lesion), T_g the mean generation time (days), and r_{max} the maximum relative growth rate (day^{-1}).

[2] Using results reported in this paper.

[3] Using data from Yeh *et al.* [1982] and Melching *et al.* [1988]

[4] Using data from Subrahmanyam *et al.* [1983] and Savary [1985]

[5] Using data from Imhoff *et al.* [1982] and Statler and McVey [1987]

Relative differences between extreme values decreased from R_o (220%), over r_{max} (65%), to T_g (23%).

Evaluation of inoculum loss in field conditions

The range of values of the exponential growth rate, r, measured in the field on different plants was 0.21–0.28 d^{-1}. The fraction of inoculum lost in field conditions, evaluated using equation (8), was, thus, 0.68–0.94 for the first leaf layer and 0.54–0.92 for the second leaf layer.

Discussion

Spore production

Sporulation curves of faba bean rust were characterized by successive sporulation peaks (Fig. 1A), as reported for the rusts of common bean [Imhoff *et al.*, 1982; Aust *et al.*, 1984], groundnut [Subrahmanyam *et al.*, 1983], and soybean [Yeh *et al.*, 1982]. Beginning 16–20 days after inoculation, we observed rings of secondary lesions surrounding the primary lesions, as reported for various legume and cereal rusts at low lesion density [Arthur, 1929; Mehta and Zadoks, 1970; Sache and de Vallavieille-Pope, 1993]. The primary lesions resulted from initial infection, whereas the secondary lesions resulted from radial hyphal growth in the leaf [Arthur, 1929]. Most primary lesions were already exhausted when the secondary sporulation peak occurred, and this peak might have been a primary sporulation peak for the secondary lesions. The production of two successive waves of spores by the primary and secondary lesions may explain why secondary peaks of sporulation were generally not observed when experimental conditions limit the infectious period beneath three weeks (e.g. Yarwood [1961]).

The sporulation rates measured on the first and second leaves of faba bean were in the same range as those measured on the first trifoliate leaf of common bean at lower lesion density [Imhoff *et al.*, 1982]. Yarwood [1961], with the same density as in our work, and Aust *et al.* [1984], with unknown lesion density, found a mean sporulation rate slightly larger than our results on primary leaves of common bean. Differences in cultivar and developmental stage of the host, isolate of the fungus, lesion density and environmental condi-

tions may explain the large range of values reported for the sporulation rate. In groundnut rust, however, the sporulation rate was not demonstrably affected by development stage and leaf age [Savary, 1987].

Infection efficiency

Mean infection efficiency of spores was 0.11 for both leaf layers. This value was in the order of magnitude (0.05–0.1) reported for common bean rust [Schein, 1964; Statler and McVey, 1987]. Variations in inoculation technique or inoculum density greatly affected the infection efficiency in groundnut rust [Savary, 1985]. The infection efficiency also varied with the developmental stage of the host and the environmental conditions [Parlevliet and Kuiper, 1977]. Variations in the infection efficiency with the age of lesions has been studied in few fungi only [Bashi and Aust, 1980; Sache and de Vallavieille-Pope, 1993]. In this study, the infection efficiency remained about constant during 20–30 days, and then sharply decreased (Fig. 2). A sharp decrease in the infection efficiency was also observed for the brown rust of wheat after four days in the infectious period [Sache and de Vallavieille-Pope, 1993]. Biological causes and consequences of variation in infection efficiency during the infectious period is not yet known.

Life-table analysis

This adaptation of life-table analysis to fungi differed slightly from Zadoks' [1977] approach. The major difference between the two approaches is related to the infection efficiency. According to Zadoks [1977], the infection efficiency had a constant value, independent of the age of the mother lesions. In our approach, the infection efficiency was age-specific, since it was evaluated for each age class of the mother lesions.

With either approach, major difficulties arise from $l(t)$ evaluation. Accurate monitoring of sporulating lesions could be achieved only at very low density, for instance after monospore inoculation. Calculations using different decreasing patterns for $l(t)$ from $t = 30$ onwards showed that life-table parameters, especially r_{max}, did not critically depend of what happened to the lesions after $t = 30$, probably because the sporulation rate and the infection efficiency were low at the end of the infectious period (data not shown).

Our approach will give an accurate evaluation of the epidemic potential because variations in infection efficiency are accounted for. Since regular measurement of the infection efficiency during the infectious period is tedious, Zadoks' [1977] approach may be advocated for the sake of practicability, assuming that variation in infection efficiency is of minor importance.

Use of life-tables for comparative epidemiology

Life-tables were built for other legume rusts, using constant infection efficiency and $l(t)$ (Table 2). *P. pachyrhizi* was characterized by a relatively long mean generation time and a relatively small maximum relative growth rate. Life-table analysis may reflect some particularities of soybean rust, such as a delayed opening of uredinia surrounded by extensive tissue necrosis, and a limited and slow sporulation [Melching *et al.*, 1979]. *U. appendiculatus* was characterized by an extremely high net reproduction rate due to high sporulation rate, and a maximum relative growth rate higher than any of the other legume rusts. Difference in ranking the pathogens according to the three life-table statistics may indicate specific interactions between monocyclic components such as latent period, infectious period, sporulation rate, and infection efficiency. Such interactions may also be caused by the host plant, as observed with *U. viciae-fabae*. On the first leaf, the net reproduction rate was smaller and the mean generation time was shorter than on the second leaf. The interaction of the two parameters resulted in a slightly higher maximum relative growth rate for the first leaf (Table 1).

Inoculum loss in field conditions

Theoretical evaluations of spore loss from plots gave conflicting figures. Van der Plank [1963] calculated that a 10 m^2 square plot would loose 24% of the produced air-borne spores. Using a simulation model, Zawolek and Zadoks [1992] showed that maximum epidemic development occurred when 16–18% of the produced spores were allocated to long-distance dispersal mechanisms. Aylor and Ferrandino [1985] estimated that 10–18% of the rust spores escaped a bean canopy. These evaluations accounted only for spores

escaping the plot. With a physical model of spore dispersal, Rijsdijk and Rappoldt [1978] showed that a 10 m^2 plot would loose about 85% of the produced spores, either by escape (65%) or soil deposition (20%). Our evaluation of spore loss agreed with the results of the physical model. The spore loss fraction ΔS depends on canopy structure, wind speed and rain leaching [Savary *et al.*, 1990]. More field studies are needed to identify factors influencing ΔS.

Life-table analysis allowed comparison of results from monocyclic growth-chamber studies, polycyclic field studies, and simulation models. This technique, which could be improved by a more precise evaluation of infection efficiency and survivorship functions, proved to be powerful in simple cases, when conditions of host and environment were not accounted for. Environment conditions were simplified by defining near-optimum conditions for the whole disease process, but each subprocess (e.g. latent period, sporulation, infection) may have slightly different optimum conditions. With further refinements and adaptations, life-table analysis could become a simple and flexible tool in comparative epidemiology at different integration levels [Kranz, 1988].

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