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A model of the early stage of epidemics

A. J. P. Oort

Laboratorium voor Fytopathologie, Landbouwhogeschool, Wageningen

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It is a well known fact that growth of a young bacterial population in a liquid medium shows a logarithmic increase, except in the very earliest stage of development. It can be compared with the growth of a capital being put out at (continuous) compound interest, and represented by the formula:

$$n_t = n_0 e^{rt}$$

in which n is the number of bacteria, t the time, e the base of the natural logarithms and r a constant indicating the rate of multiplication. For increase of populations of fungal pathogens of the leaf spot type (e.g. rusts, downy or powdery mildews) on its hosts this simple formula is not satisfactory, and the following has to be considered. When a single spore has arrived on a leaf under suitable conditions an infection occurs. After a latent period[1] of p days the mycelium in the infected area starts to sporulate and does so during an infectious or sporulating period[1] of i days. This leads to new infections with a multiplication rate m expressed in the number of successful daughter infections per mother infection per day. Each daughter infection on its turn starts sporulating after p days at a multiplication rate m during i days and so on. For further considerations it is assumed that each day environmental conditions are equally suitable for development, sporulation and infection, without being necessarily constant. Also it is assumed that within the space under consideration the spores are evenly distributed and the substrate is not a limiting factor. For combinations of two values of p, m and i, respectively, making possible eight different combinations, the development of epidemics has been calculated. The time unit chosen was a day. For simplification of calculations the values chosen were small viz. 2 and 5, smaller than the values occurring in natural systems. The results of the calculations are given in Fig. 1 in which the logarithm of the cumulative total of infections n is plotted against time.
When the latent period is long ($p = 5$) and the infectious period short ($i = 2$) the successive "generations" are well established and do not overlap each other, and the increase progresses in distinct waves. In the long run the waves fade away and the increase approximates a straight line on a log scale. Even in the cases of $i = 5$ the increase initially shows some fluctuations. When on the other hand the latent period

[1] Latent period (p) and infectious period (i) are used in accordance with van der Plank (1963, p. 41 and 99).

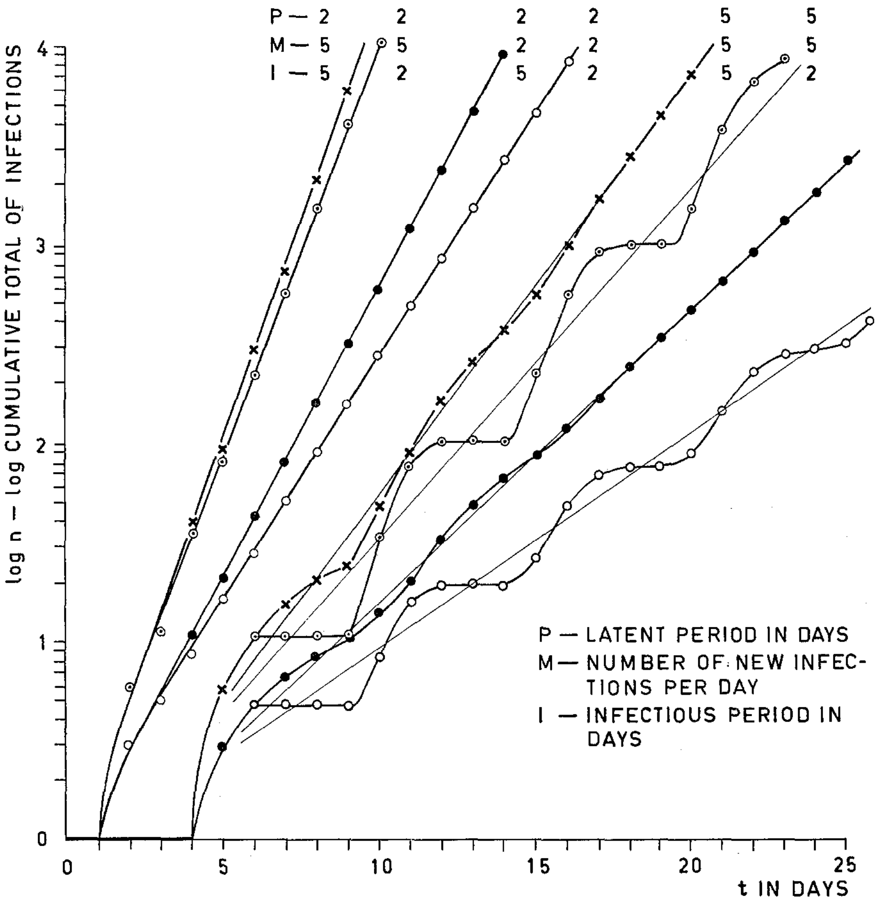

Fig. 1. Effect of latent period, number of new infections and infectious period on the increase of a fungus population

is short (p = 2) the generations overlap each other right away and the increase results in a straight line from the beginning on.

It is clear that the rate of increase of the population (progress of the epidemic) is highest when p is small as compared with m and (or) i, and lowest when p is large as compared with m and (or) i.

One may ask whether under field conditions in the beginning of epidemics infection waves as mentioned above can be demonstrated. During summer when conditions are favourable for the rapid development of epidemics generally the latent period is relatively short and the infectious period long so that overlapping of generations can be expected. Waves in the multiplication of pathogens which are observed, as for instance with *Phytophthora infestans*, usually have to be ascribed to alternating periods of suitable and less suitable climatic conditions.

During winter and early spring when p is long to very long and i – as a result of frequent adverse weather conditions – short consecutive generations may be expected to remain distinct and therefore may be demonstrable. In his studies on wheat yellow

Table 1. Explanation see text. (After Corsten, 1964)

p	m	i	$1/x_1$	$\{x_1+pmx_1^p - (p+i)mx_1^{p+i}\}^{-1}$	$(-\log x_1)^{-1}$
5	2	2	1.288	0.8220	9.099
5	2	5	1.412	0.5395	6.671
5	5	2	1.526	0.5377	5.447
5	5	5	1.637	0.4210	4.671
2	2	2	1.769	0.9745	4.037
2	2	5	1.977	0.7103	3.378
2	5	2	2.627	0.7099	2.384
2	5	5	2.784	0.6164	2.249

rust (*Puccinia striiformis*) Zadoks (1961) found waves in the early stages of development of this pathogen, which might be explained in this way. It must be kept in mind, however, that here too climatic conditions may play a part, so that the fluctuations in the progress of the epidemic generally may be the result of combined effects, both of generations and climate.

A mathematical solution for the model introduced above has been established by Corsten (1964). He developed an equation from which for the one positive simple root x_1 an other equation can be derived, which is given here.

$$\log n_t = -\log\left\{x_1+pmx_1^p - (p+i)mx_1^{p+i}\right\}+t.\log\frac{1}{x_1}$$

This equation makes it possible to calculate for any combination of values of p, m and i the slope of the line describing the progress of the epidemic in the long run.

The greater t, the better the approximation of $\log n_t$ by the above equation, a linear function in t with $\log (1/x_1)$ as slope and $\{x_1 + pmx_1^p-(p+i)mx_1^{p+i}\}^{-1}$ indicating the point of intersection with the $\log n_t$ axis. For values 2 and 5 the root x_1 has been calculated with an IBM computer and the slopes have been determined using this asymptotic formula. The slopes are in good agreement with the calculations mentioned in the first part. In Fig. 1 they are indicated by thin straight lines. In Table 1, copied from the publication of Corsten, the corresponding values of $1/x_1$ and of $(-\log x_1)^{-1}$ for the eight combinations of values of p, m and i are given in columns 4 and 6, respectively. The values $1/x_1$ are the factors with which the population increases daily by good approximation. The values of $(-\log x_1)^{-1}$ can be used for the graphic determination of the slope of the approximating line, considering that an increase of one unit on the $\log n_t$ scale (for instance from 10^2 to 10^3) corresponds with an increase on the t scale of $(-\log x_1)^{-1}$ units. The values of the fifth column indicate the point of intersection with the n_t-axis.

Samenvatting

Een model voor het eerste stadium van epidemieën

Een model, dat de ontwikkeling van een epidemie van pathogene schimmels van het vlekkentype (bijv. roesten, echte of valse meeldauwschimmels) beschrijft, moet rekening houden met de duur van de latentieperiode p en van de sporulatieduur i beide in dagen en tevens met een vermeerderingsfactor m uitgedrukt in het aantal geslaagde dochterinfecties per moeder-infectie per dag. Voor twee waarden van resp. p, m en i, namelijk 2 en 5, die klein zijn gekozen om de berekeningen te vereenvoudigen, is het verloop van de epidemie uitgerekend. Wordt de logarithme van het cumulatieve totaal van de infecties n uitgezet tegen de tijd, dan ontstaat een lijn, die zeer snel tot een rechte nadert, behalve wanneer de latentieperiode p lang is vergeleken bij de sporulatieduur (Fig. 1). Op de consequenties van het voorgaande voor natuurlijke epidemieën wordt gewezen.

Door Corsten is een mathematische oplossing voor het model opgesteld (zie formule) die het mogelijk maakt met behulp van een computer voor elke combinatie van waarden van p, m en i de plaats en richting van de rechte te bepalen waartoe de epidemie nadert. Voor de waarden 2 en 5 zijn deze berekend (Tabel 1). Zij zijn in goede overeenstemming met de in het eerste gedeelte genoemde berekeningen.

References

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