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STUDIES OF YIELD LOSSES I. THE SELF-LIMITING EFFECT OF INJURIOUS OR COMPETITIVE ORGANISMS ON CROP-YIELD[1, 2]

Met een samenvatting: Studiën over oogstverlies I. Het effect van concurrentie tussen schadelijke organismen bij toenemend aantal

BY

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INTRODUCTION

An increase in the initial number of injurious organisms or local infections is not necessarily followed by a proportionate loss in yield of the crop involved. The effect per individual decreases as the numbers increase and thus is density dependent. This phenomenon has been observed with root eelworms where crop yield or growth varies inversely with the logarithm of the initial population level (JONES, 1956, 1957, for *Heterodera schachtii* SCHM.; LOWNSBERY & PETERS, 1955, for *H. tabacum* LOWNSBERY & LOWNSBERY). For the Hessian fly it was described by HILL, UNDINE and PINCKNEY (1943) in relation with the number of puparia per wheat culm.

A similar phenomenon can also be observed for competition between plants of the same species in spacing experiments on crop plants (e.g. DUNCAN, 1958, for maize).

The principle of the self-limiting effect is discussed below with the aid of four hypothetical models representing natural phenomena in such a way that the effects may be assessed mathematically. In all examples it is supposed that the organisms do not migrate to other plant parts, once they are settled.

In another paper the reaction of the plants to the rate of injury will be discussed by the second author.

MODEL I

In Fig. 1 a rootlet is infected simultaneously at the places A, B and C. Each infection is capable of killing the root at the point of infection. Because of its position the infection at A overrules the other two and the length of the remaining healthy portion depends on the point of infection that is farthest away from the root tip. If the chance of infection at a point within a given interval is proportional to the length of the interval the following relation is established:

$$R = \frac{L}{n + 1},$$

where R is the remaining healthy part of the rootlet, L the initial length of the rootlet and n the number of infections per rootlet.

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[2] For the mathematics the reader is referred to the appendix.

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In Fig. 2, R expressed as a percentage of L is plotted against n.

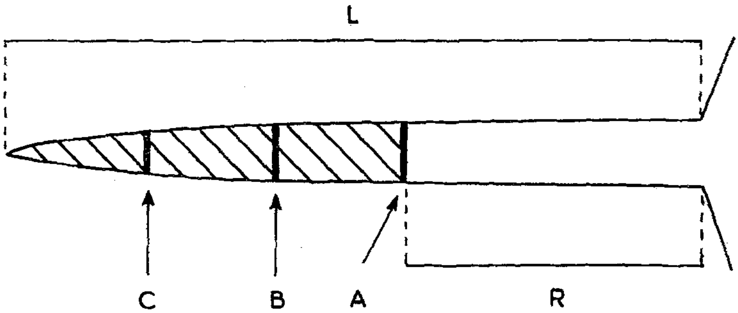

Fig. 1. For explanation see text.

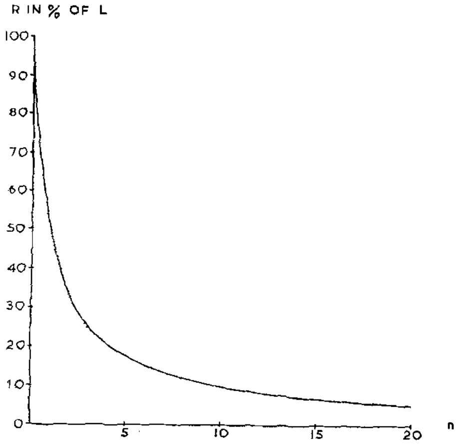

Fig. 2. For explanation see text.

MODEL II

Suppose that seeds are attacked at random by larvae of beetles, e.g. beans by *Acanthoscelides obtectus* SAY. When there are the same number of seeds and larvae, most seeds will be invaded by one larva, some by two and even a few by three larvae or more, but there will be a number of seeds that are free from infection. The chances for each seed being attacked by a larva are supposed to be equal, regardless of the results of former attacks. Then the expected percentage of uninfected seeds can be approximated by:

$$2.718^{-\alpha} \times 100,$$

both the number of seeds n and of larvae r being large and $\alpha = \frac{r}{n}$.

In Fig. 3 the relation between the percentage of healthy seeds and the number of beetles per 100 seeds is graphically represented.

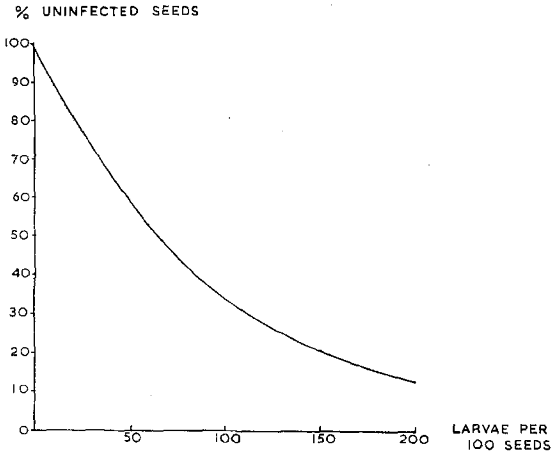

Fig. 3. For explanation see text.

Fig. 4. For explanation see text.

Model III

Suppose that leafspots of a definite size caused by an infection overlap when present in large numbers (Fig. 4). If again the chances of infection within a given leaf area is proportional to the area regardless of former infections, the leaf spots will overlap and the expected non-damaged area may be shown to be:

$$r \times (1 - \alpha)^n,$$

where r is the remaining free leaf surface and $\alpha = \frac{s}{m}$, s being the surface area of a spot and m the surface area of a leaf and n the number of spots per leaf. This formula was developed for bombing patterns during the war (Garwood, 1947).

Graphic representation between r, expressed as a percentage, and n is given in Fig. 5 for spots, each of which covers 1/10 of the area of a leaf.

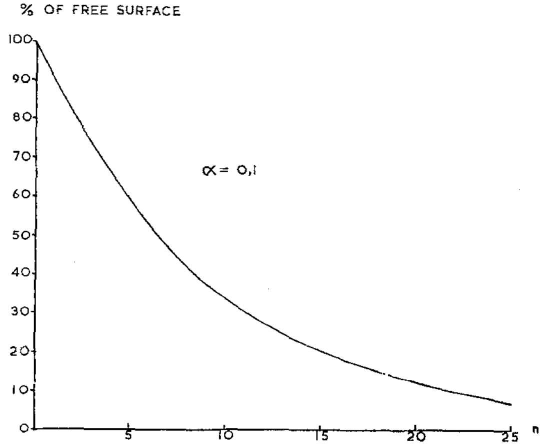

Fig. 5. For explanation see text.

MODEL IV

In spacing experiments with crops, the yield per square metre increases in proportion to the number of plants per unit area as long as there is ample spacn for development of each plant. However, as soon as plants are in competitioe for soil space, water or light the yield per square metre is the same for quite a wide range of plant population densities. For peas, RIEPMA (1953) observed that the total yield per unit area did not change over the range from 25 to 167 plants per square metre. Over this range yield of individual plants is directly proportional to the surface area they occupy.

Not taking in account possible yield depressions due to very dense planting,

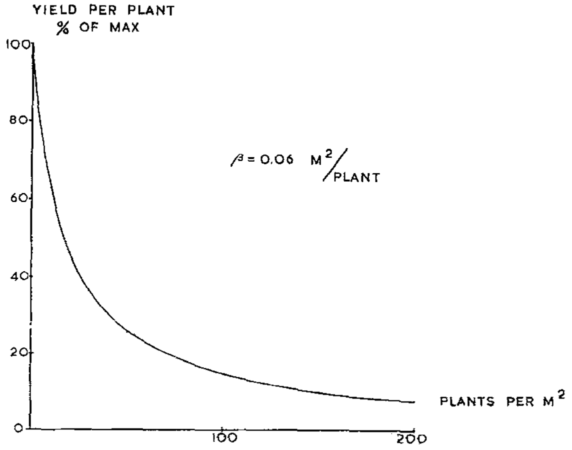

Fig. 6. For explanation see text.

DE WIT (1960) used the following formula for the relation between the yield per plant *(a)* and the number of plants per square metre *(n):*

$$a = \frac{\beta}{\beta n + 1}\,\Omega,$$

in which Ω is the (extrapolated) yield per unit area at very high plant densities and $\beta\Omega$ the extrapolated yield of one plant growing far apart from any other plant.

A graphic representation of the yield per plant in relation to the number of plants per square metre is given in Fig. 6.

It is often not realised that, when the area occupied by a plant becomes smaller, its influence on its neighbours decreases and this, in fact, can be the self-limiting effect of increasing population density. Similarly, the effect of ten weeds on a surface area may be much smaller than ten times the effect of a single weed in the same area.

DISCUSSION

The above mentioned models and their mathematical formulae show how competitive forces may act and limit the effect of increasing numbers of injurious organisms or infections. The harmful effect of the individual decreases as their numbers increase and, as a result, the linear correlation between numbers and injury may decrease as high population densities occur. Intraspecific competition not only reduces the effect upon yields, but may also affect the injurious organisms themselves, e.g. by decreasing their rate of multiplication, so reducing the final population. The multiplication rate of *Heterodera rostochiensis* WOLL. is strongly limited at high densities of eelworm populations (OOSTENBRINK, 1950). HESLING (1957) has also observed that the multiplication rate (cyst efficiency) of *Heterodera avenae* WOLL. decreased with an increase in the eelworm population as also has JONES (1956) for *Heterodera schachtii* SCHM.

In nematodes, competition not only causes death of individuals, it may also affect the sex ratio (ELLENBY, 1954; TRIANTAPHYLLOU & HIRSCHMANN, 1959).

The question of multiplication is obvious in spacing experiments as a density dependent factor.

SUMMARY

Four hypothetical models illustrate how competition between pathogens diminishes the effect of individuals as numbers increase. As a result the relation between crop yield or growth and the initial population level is not linear. The effect on yield falls off as the initial population increases or when graphed the yield curve tends to become horizontal.

SAMENVATTING

Aan vier modellen wordt duidelijk gemaakt, hoe concurrentie tussen schadelijke organismen de invloed van het individu op de waardplant kan verminderen. Als gevolg daarvan zal de relatie tussen het aantal organismen en de oogstderving of de groei niet rechtlijning zijn. Het effect wordt relatief minder als het aantal schadelijke organismen stijgt. In een grafiek heeft de lijn de neiging om horizontaal te worden bij hogere aantallen organismen, bijvoorbeeld fig. 6 (oogst verticaal, schadelijke organismen horizontaal).

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APPENDIX

Model I: We are given a line of lenght L with n points chosen at random on the line, and assume that the stochastic variable $\underline{x}_i$, the distance of point i from an endpoint, has a rectangular distribution.

If the first point chosen is $\underline{x}_1$ the expectation of $\underline{x}_1$, under the condition that $\underline{x}_2, \dots \underline{x}_n$, are all smaller or equal to $\underline{x}_1$, is:

$$E(\underline{x}_1) = \int_0^L \frac{\underline{x}_1}{L} d\underline{x}_1 \int_0^{x_1} \frac{dx_2}{L} \cdots \int_0^{x_1} \frac{dx_n}{L} = \int_0^L \frac{x_1}{L} dx_1 \left[\int_0^{x_1} \frac{dx_i}{L} \right]^{n-1} = \frac{1}{L^n} \int_0^L x_1^n \, dx_1 = \frac{L}{n+1} .$$

However, we want the expectation of $\underline{x}_i$ regardless of the value of i and as every $\underline{x}_i$ has equal chance of taking the largest value we obtain

$$E(\underline{x}) = \frac{n}{n+1} L \quad \text{and} \quad E(R) = L - \frac{n}{n+1} L = \frac{L}{n+1} .$$

Model II: This model is analogous to the so-called occupancy problem which may be stated as follows;

r marbles are distributed over n boxes in such a way that every marble has an equal chance of going into any one of the n boxes.

What is the probability that m boxes remain empty? What is the expectation of the number of empty boxes?

The solution, the derivation of which is somewhat lengthy, is given by FELLER (1957, pg. 58).

$$P_m (r, n) = \binom{n}{m} \sum_{\nu=0}^{n-m} (-1)^\nu \binom{n-m}{\nu} \left(1 - \frac{m+\nu}{n}\right)^r .$$

The expectation is obtained by multiplying $P_m (r, n)$ by n^r. In the biological problem we are interested in the case that both r and n are large and $r/n = \alpha$ (constant). In that case the distribution approximates the Poisson with $\lambda = ne^{-\frac{r}{n}}$ expected number of empty boxes.

The percentage empty boxes is then $100\ e^{\frac{r}{n}}$.

Model III: Let the area of the leaf be m cm² and the area of the leafspot caused by one infection s cm², and $s/m = \alpha$. The probability that a given point A is outside the area damaged by the first infection is $(1 - \alpha)$; the probability that it is outside the total area damaged by n infections is $(1 - \alpha)^n$ which is then the expected proportion of the leaf that is undamaged.

Clearly the percentage damage depends on α. If α is not small, it is not permissible to neglect the influence of the margin of the leaf as has been done in the above.

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