PRINCIPLES OF MEASURING CROP LOSSES IN COMPETITIVE SITUATIONS WITH PARTICULAR REFERENCE TO WEEDS

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SUMMARY

A theory is presented by which it is possible to calculate the effect that plant species in a mixed culture have on each other's growth. Basic data are provided by a spacing experiment with the species in monoculture. Calculated and actual results are compared for mixtures of barley and oats and of long and short peas.

This theory makes it possible to estimate crop losses due to weed infestation and the influence of cultivation practices thereon, without covering the whole range of interest by experiments.

It is also shown that the growth reduction due to viruses, nematodes and low soil pH can be accentuated by growing the species in competition with another selection, variety or similar species free of viruses, resistant to nematodes or tolerant to low pH. This technique can be used conveniently for screening purposes.

INTRODUCTION

Crop losses due to weeds vary greatly. Where weed infestation is light and the crop makes an earlier growth than the weeds, the crop may crowd out the weeds, and the damage is small. Where, however, due to a delay between the preparation of the seedbed and the actual sowing, weeds germinate earlier, a small infestation may lead to considerable losses. There are also situations where the initial damage is high, but the weeds starve later due to a vigorous growth in height of the crop. The reverse may also be true. Many case histories illustrate these effects, but these do not help much when it comes to estimating the crop losses due to weed infestation and the influence of cultivation practices thereon.

During a sabbatical leave of the second author at the I.B.S., an approach was developed - to be published elsewhere - which enables the estimation of crop losses due to competition, taking into account the time of germination and plant density on the basis of the growth of the species in monoculture. This approach forms a basis for the analyses of competitive phenomena during the establishment of grass swards, but can also be used to study competitive phenomena between a crop and weeds.

It is a development of a theory on plant competition by DE WIT, VAN DEN BERGH, ENNIK and TOW (1958, 1960, 1965, 1966). This theory has been used also to analyse in more detail the influence of diseases on growth of crops. Especially, the weed and disease aspects will be considered in this paper.

THE WEED ASPECT

The yield of a plant species planted or sown at low densities and during the earlier stages of growth is almost proportional to the number of plants in the field. At normal sowing densities, instead, the yield approaches a maximum with an increased number of plants and it may decrease again at very high densities. Leaving aside the extremes, this saturation type of curve may be presented by the formula:

$$O = \frac{Z}{\beta Z + 1} \beta \Omega \qquad (1)$$

in which Z is the density of sowing or planting (for instance in kg/ha, plants/m^2, rows/meter) and O the yield (in kg dry matter/ha, kg seed/ha, and so on). The constant Ω represents the (extrapolated) yield at high seed densities and the value β, expressed in the inverse unit of the seed rate, characterizes the degree of saturation. The yield increases almost proportionally to the seed rate when βZ is small compared with 1, and is almost independent of the seed rate when βZ is large compared with 1.

The (extrapolated) yield of one plant or one single row of plants growing far apart from other plants or rows is equal to the product of β and Ω, as can be shown by dividing the yield O by the planting density Z and taking the limit for Z

approaching to zero:

$$\lim_{Z \to 0} \frac{O}{Z} = \lim_{Z \to 0} \frac{\beta\Omega}{\beta\Omega + 1} = \beta\Omega \qquad (2)$$

The relative yield or the occupied space in relative units defined as the quotient of O and Ω is

$$o = \frac{O}{\Omega} = \frac{\beta}{\beta Z + 1} \qquad (3)$$

and varies from 0 to 1.

By taking again the limit for Z approaching to zero, it is evident that β is the "space" occupied by one plant or row in the absence of competition. By harvesting spacing experiments at various time intervals it has been found that the values of $\beta\Omega$ and β increase with time. This is shown in Figure 1, which is based on experiments with barley, oats, and short and long peas grown in rows spaced at 25 and 100 cm. The yield per plant ($\beta\Omega$) increases according to expectation more or less exponentially with time. The curves for β show that barley claims space especially during the earlier periods of growth, but that during the later stages it is surpassed by oats. Short and long peas at first claim space at the same rate, but later long peas lead. The property to claim space during early growth is, of course, of primary importance in competitive situations.

To develop an approach which enables a calculation to be made from these basic plant characteristics of their mutual influence, a procedure must be introduced to calculate the yield at the (t+1)-th day from the yield at the t-th day. Equation (3) can be rewritten with the seed rate Z given explicitly:

$$Z = \frac{o_t}{\beta_t (1 - o_t)} \qquad (4)$$

in which the indices indicate which variables are time-dependent.

The relative yield at the (t+1)-th day is equal to:

$$o_{t+1} = \frac{\beta_{t+1} Z}{\beta_{t+1} Z + 1} \qquad (5)$$

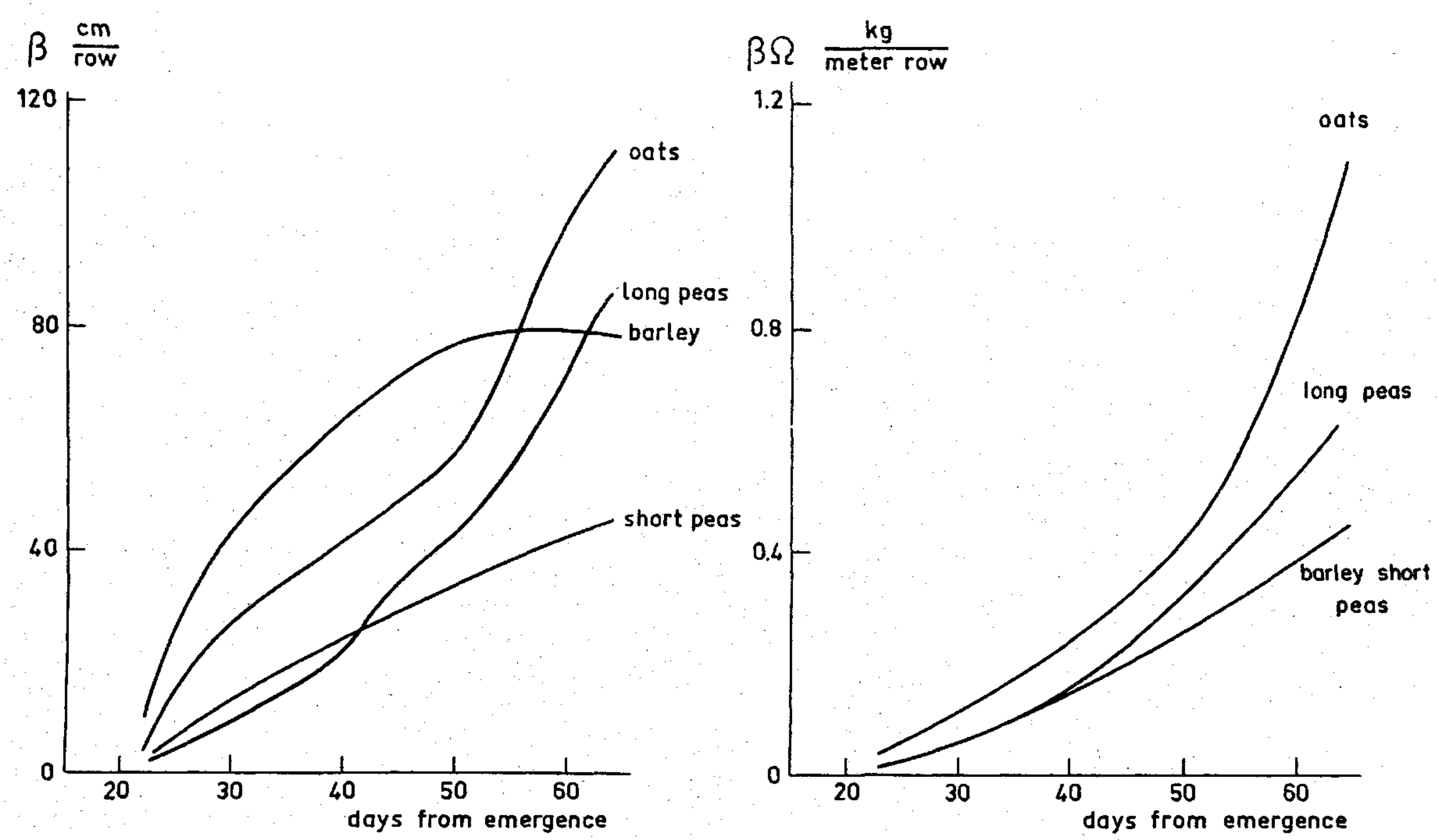

Figure 1. (Baeumer and de Wit, unpublished)

By substituting the value of Z out of equation (4) in equation (5), an expression is obtained which shows how the relative yield at the (t+1)-th day depends on the relative yield at the t-th day:

$$\sigma_{t+1} = \frac{\beta_{t+1}}{(\beta_{t+1} - \beta_t)\ \sigma_t + \beta_t}\ \sigma_t \qquad (6)$$

There are two ways of calculating the relative yield at the n-th day. At first the values of β and $\beta\Omega$ can be read from Figure 1 for the n-th day and substituted in equation (3) with the proper value of Z. The other way is to give an initial value for σ at the first day instead of the value of Z, read the value of β for the first and second day, and obtain the relative yield at the second day by means of equation (6). This procedure can be repeated until the n-th day is reached. This step by step advancing in time or simulation is cumbersome, but it enables one to take account of the mutual influence of two plant species grown in competition.

The denominator of equation (6) characterizes the degree of intra-specific competition at the t-th day. At the earlier stages, σ_t is small compared with 1 and intra-specific competition is absent. However, the importance of σ_t in this term increases in course of time so that the daily increase in σ_t becomes negligible when σ_t approaches one. The intra-specific competition is then in full force.

The assumption that two species feel each other's presence in the same way as their own leads to the following equations:

$$O1_{t+1} = \frac{\beta 1_{t+1}}{(\beta 1_{t+1} - \beta 1_t)(\sigma 1_t + \sigma 2_t) + \beta 1_t}\ \sigma 1_t$$

for the first, and (7)

$$O2_{t+1} = \frac{\beta 2_{t+1}}{(\beta 2_{t+1} - \beta 2_t)(O2_t + O1_t) + \beta 2_t}\ \sigma 2_t$$

for the second species.

This interference with each other's growth is here accounted for by replacing $O1$ and $O2$ in the denominators by $O1 + O2$. Hence, when the sum of the relative yields of both species approaches 1, none of them is able to increase any more so that the species cannot encroach on each other's space. The absolute yields at the t-th day are close to:

$$O1_t = \sigma 1_t \cdot \Omega 1_t$$
$$O2_t = \sigma 2_t \cdot \Omega 2_t \qquad (8)$$

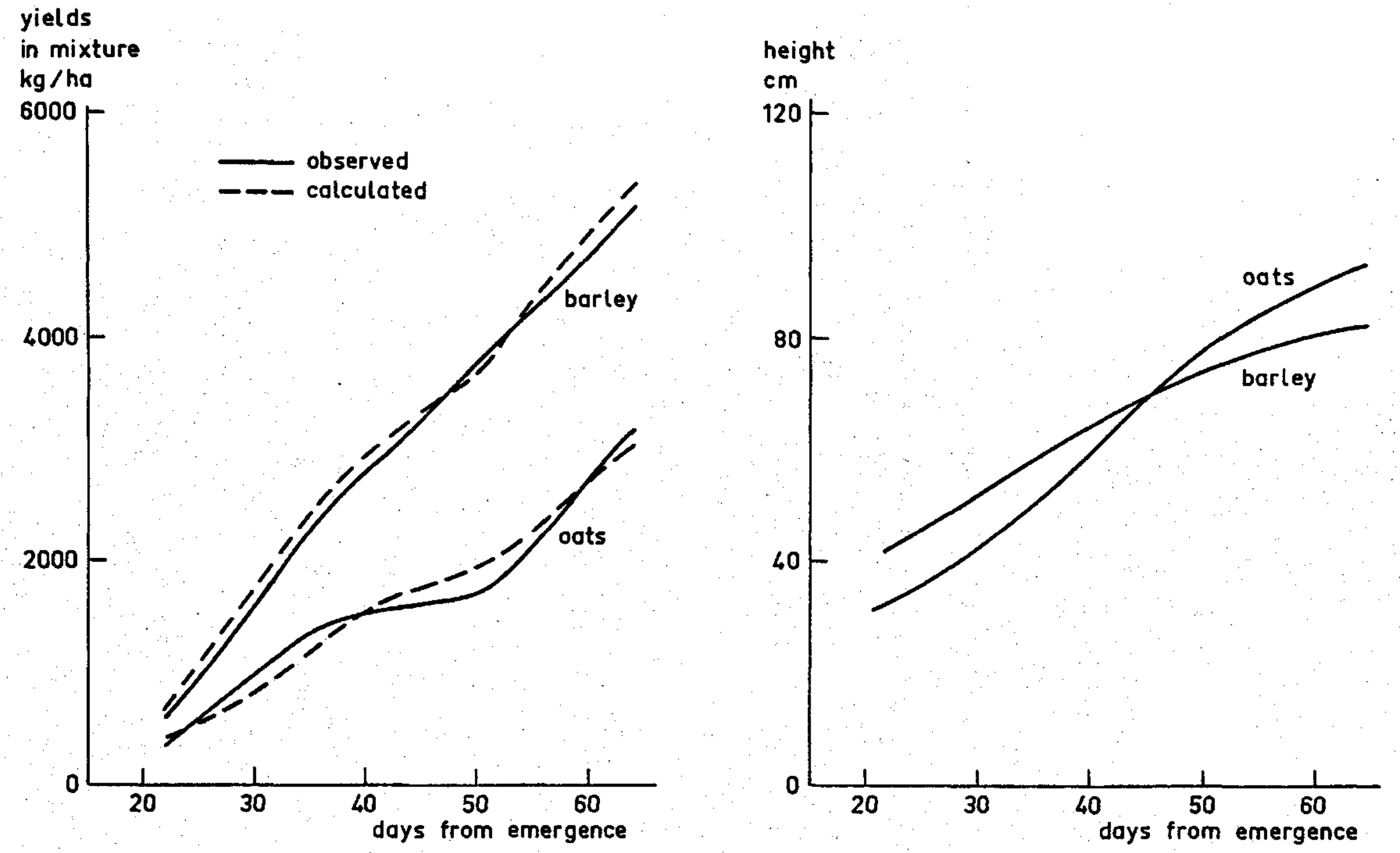

Figure 2. (Baeumer and de Wit, unpublished)

Because Ω_1 and Ω_2 may continue to increase with time even when the sum of the relative yields is 1 or the space is fully occupied, the yields in the mixtures may also continue to increase.

The values of β for barley and oats can be read now in Figure 1 at the 22nd day after emergence. At this early stage, the mutual influence is still absent, so that the relative yields of barley and oats when both are sown alternately in rows of 25 cm, can be calculated by substituting these values for β and a value of 2 rows/meter for Z in equation (3). These answers are used to calculate the relative yields at the second day with equation (7), and by subsequent recursive use of these equations the time dependent course of both relative yields is obtained. These relative yields can be converted into absolute yields by using equations (8) and values of Ω derived from Figure 1.

The simulated course of yields of both species - one being the weed of the other - is presented in Figure 2 (left) by the dotted lines. Although both species are planted in a 1:1 proportion, the yield of barley in the mixture is calculated to be about double. This is due to its ability to claim space during the earlier stages of growth. Oats never gets a chance because by the time it starts to claim space, most space is already occupied. The actual experimental yield courses are presented by the solid lines. The agreement between the simulated and experimental results is so good that it can be concluded that these two plant species interfere according to the simple scheme presented by the equations (7).

One reason why this simple procedure does so well is that the growth in height of both species (Figure 2, right) is about the same, so that one species cannot encroach upon the other by intercepting a disproportionate amount of light.

This is quite different in the case of short peas and long peas, especially when - as in our experiments - the long peas were held upright by wire gauze. Figure 3 (left, solid lines) gives the observed yields and the yields (dashed lines) calculated according to equations (7). Both species match each other, according to the calculation which is in agreement with the same form of the curves of β and $\beta\Omega$ during the earlier stages in Figure 1. However, in the actual case long peas take practically the whole field and this is undoubtedly due to the large difference in height (Figure 3, right) and the resulting disproportionate distribution of light.

This encroachment of one species upon the other can be accounted for in first approximation by multiplying the relative yields of the other species in the equations (7) by a factor x and 1/x, respectively. This gives:

$$o1_{t+1} = \frac{\beta 1_{t+1}}{(\beta 1_{t+1} - \beta 1_t)(O1_t + x_t \cdot O2_t) + \beta 1_t} o1_t$$

for the first, and

$$o2_{t+1} = \frac{\beta 2_{t+1}}{(\beta 2_{t+1} - \beta 2_t)(O2_t + \frac{1}{x_t} \cdot O1_t) + \beta 2_t} O2_t \qquad (9)$$

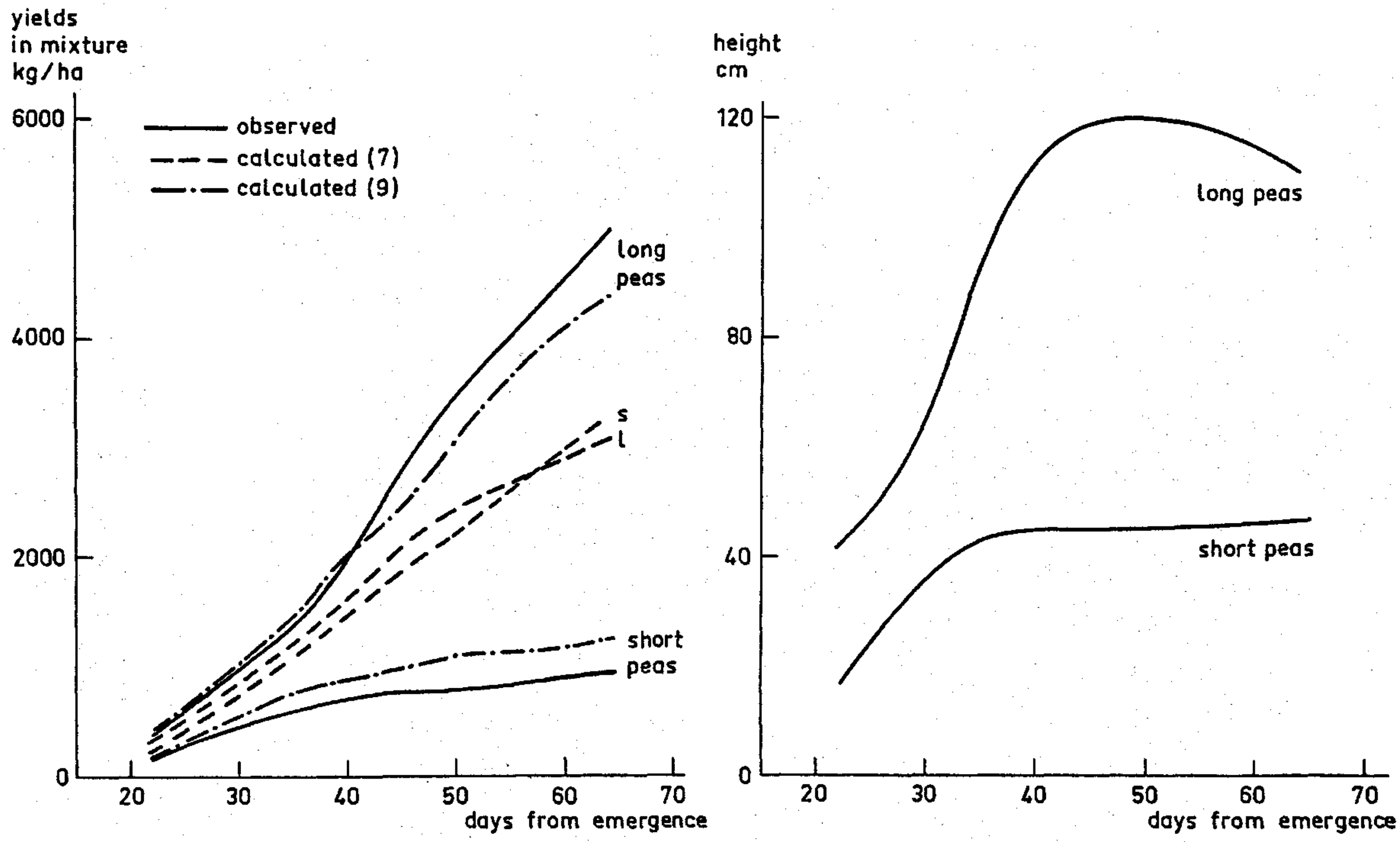

Figure 3. (Baeumer and de Wit, unpublished)

for the second species. This multiplication factor x implies that the interference of species 2 with species 1 is x times larger than can be expected from its relative yield, and the interference of species 1 with species 2 accordingly x times smaller. (It should be noted that these equations are analogous to the well-known Lotka-Volterra equations for competition, with the difference that here the relative rate of increase ($\frac{1}{\beta} \frac{d\beta}{dt}$) is a function of time).

The difficulty is to find a reasonable estimate for x. At present, the ratio in height of both species at each time step is chosen. The yield curves calculated by means of equation (9) on the basis of this choice are also given in Figure 3. The agreement with the observed curves is perhaps too good, considering the rough procedure.

The same method may be used to estimate crop losses due to weeds. It is necessary to grow the crop and the weed species at two densities not too far apart from the practical situation and to determine the yields at suitably chosen intervals. It is allowed to broadcast the weeds and to sow the crop in the customary way because,in subsequent calculations, the seed density and the way of sowing do not enter as such in the equations (7) and (9). The procedure may be extended to calculate the mutual interference of more than two species, and experiments with three grass species are under way to show that this is indeed the case. Application of this simulation procedure in weed research makes it unnecessary to grow the species in mixtures at all practical important combinations of degree of infestation and germination time, and enables also to simulate the effect of weeding or herbicide applications during the growth of the crop. These simulations are most conveniently done by means of a computer and the necessary FORTRAN programs to execute them have been developed.

The yields of barley and oats have been calculated in a replacement series as an example of this. This is a situation in which the sum of the relative seed rates of the species in a mixture, calculated with respect to their seed rates in monoculture, is kept at one. It follows from equation (7) that the relative yield total, which is the sum of the relative yields in the mixtures calculated with respect to the yields in monoculture, is approximately one. This is shown by the solid lines in Figure 4, of which the one for oats is curved downward, and the one for barley curved upward to the same extent. These lines hold for a planting density of 4 rows per meter, and for sowing at the same time, the field being harvested 64 days after sowing. Barley is obviously the most agressive species, as was found earlier (Figure 2). However, when the growth of barley is postponed one week, the field still being harvested 62 days after the sowing of oats, the latter is most agressive.

THE DISEASE ASPECT

The reduced capability of plants to grow due, for instance, to virus diseases, nematodes or a low soil pH, is often not reflected in the final yield, because the planting density is so high that even with a reduced growth, all space is claimed at an early stage. To observe large effects, it is better to grow the plants at wide densities, but this is often not feasible, especially in greenhouse experiments. Instead, the extent of the damage may be enhanced by growing the plant species in a replacement series with another selection, or a variety of similar

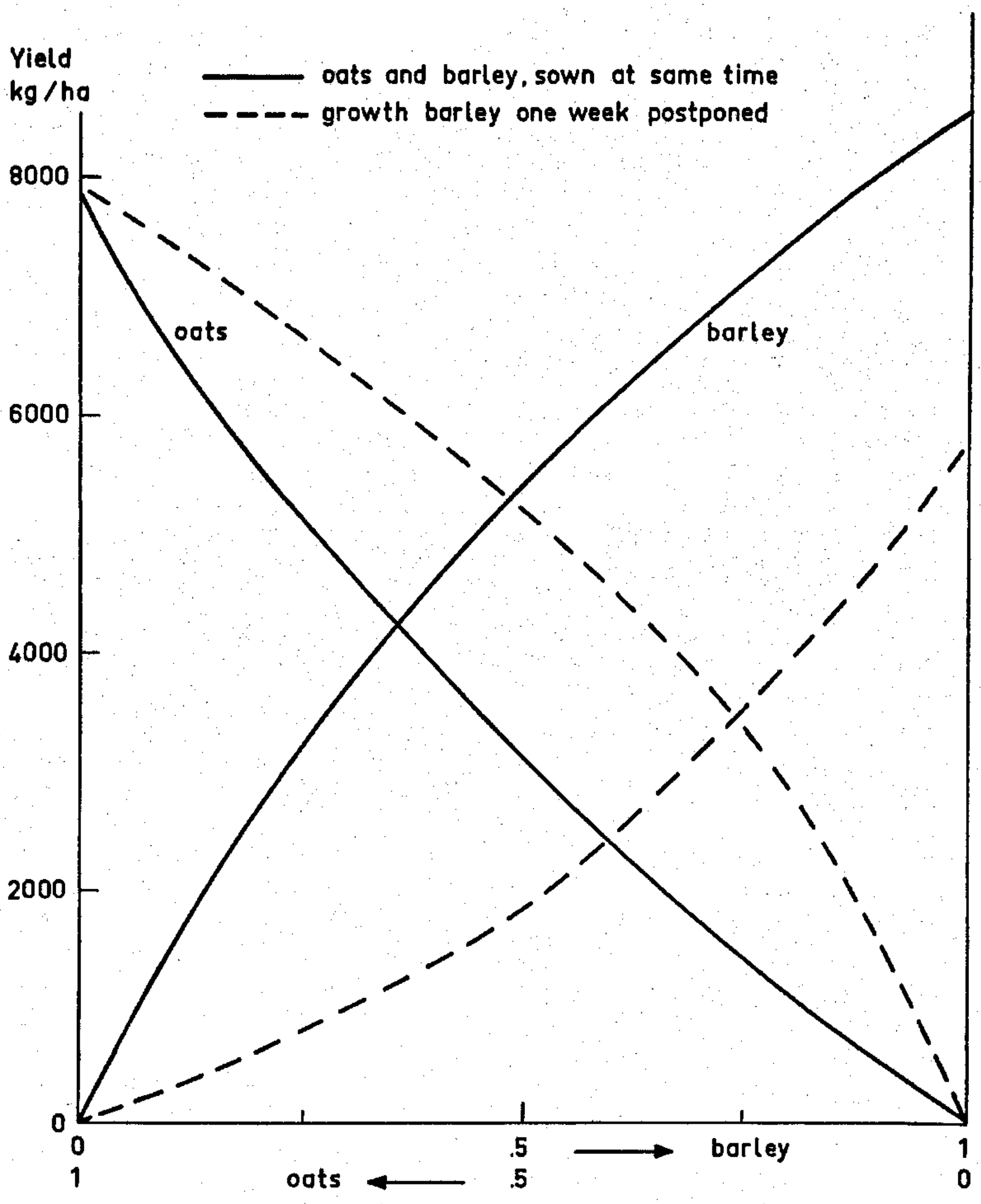
Yield
kg / ha
oats and barley, sown at same time
growth barley one week postponed
8000
6000
4000
2000
0
oats
barley
0
1
.5
.5
barley
oats
1
0

Figure 4.

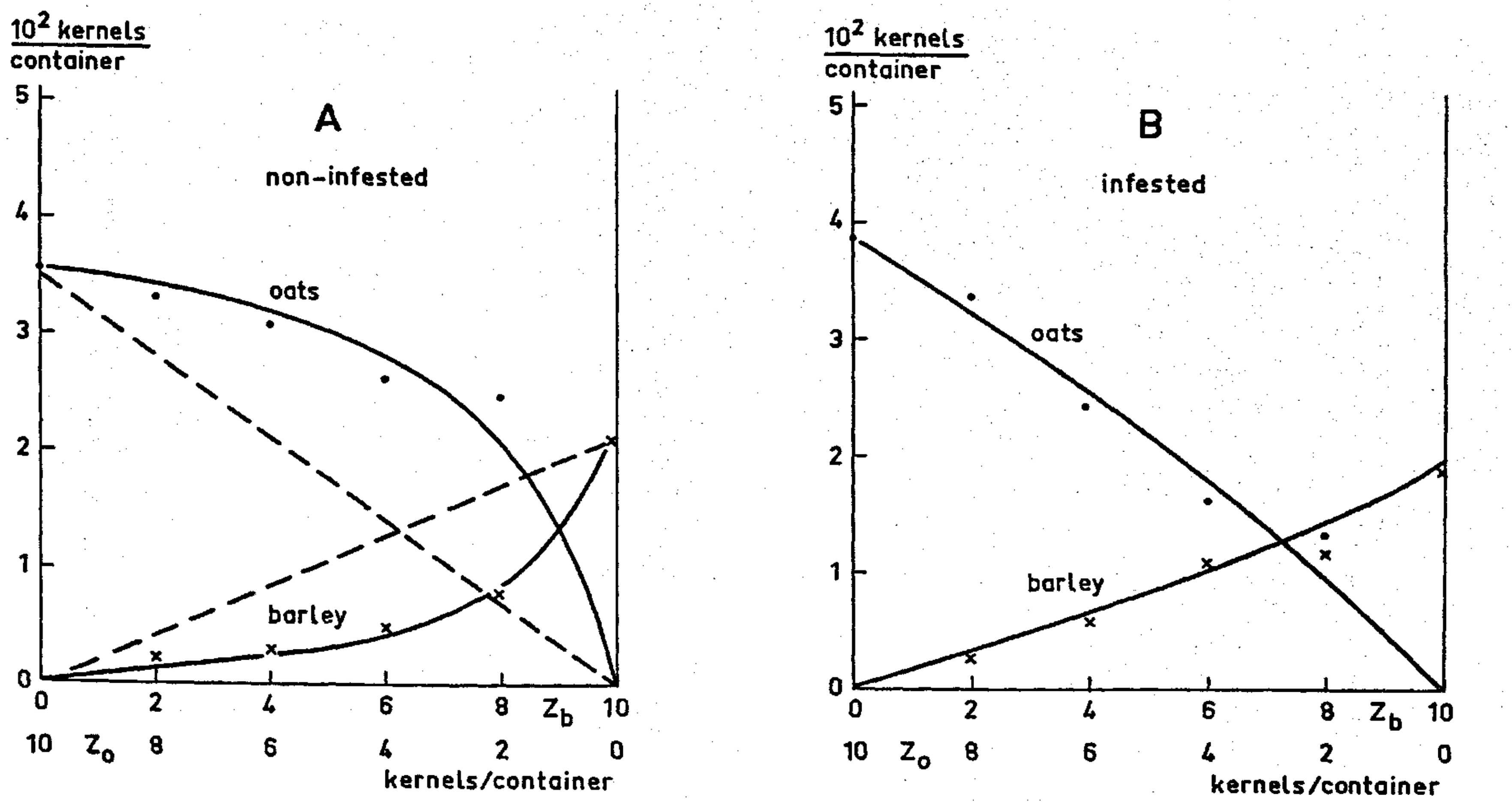

Figure 5. (Sibma, Kort and de Wit, 1964)

species which is free of viruses, resistant to nematodes or tolerant to low pH. A few examples of this important phenomenon are given.

Oats are susceptible to nematodes, but yield differences between oats on infested and non-infested soil are rare, at least under greenhouse conditions. However, when oats are grown in a replacement series in competition with a nematode-tolerant barley, the yield damage may be very marked. This is illustrated in Figure 5 where (left) are given the yields of a replacement series on a non-infested soil, and (right) the yield on infested soil. The yield of oats in monoculture is the same under both conditions, while that in the mixture on the infested soil is lower than on the non-infested soil. The reverse is the case for barley.

Barley is much more susceptible to a low soil pH than oats, but the results of the experiment shown in Figure 6, where replacement series in a soil brought to a pH-KCl of 4 and 3.7 are reproduced, indicate that this effect of pH is much more pronounced in the competitive situation.

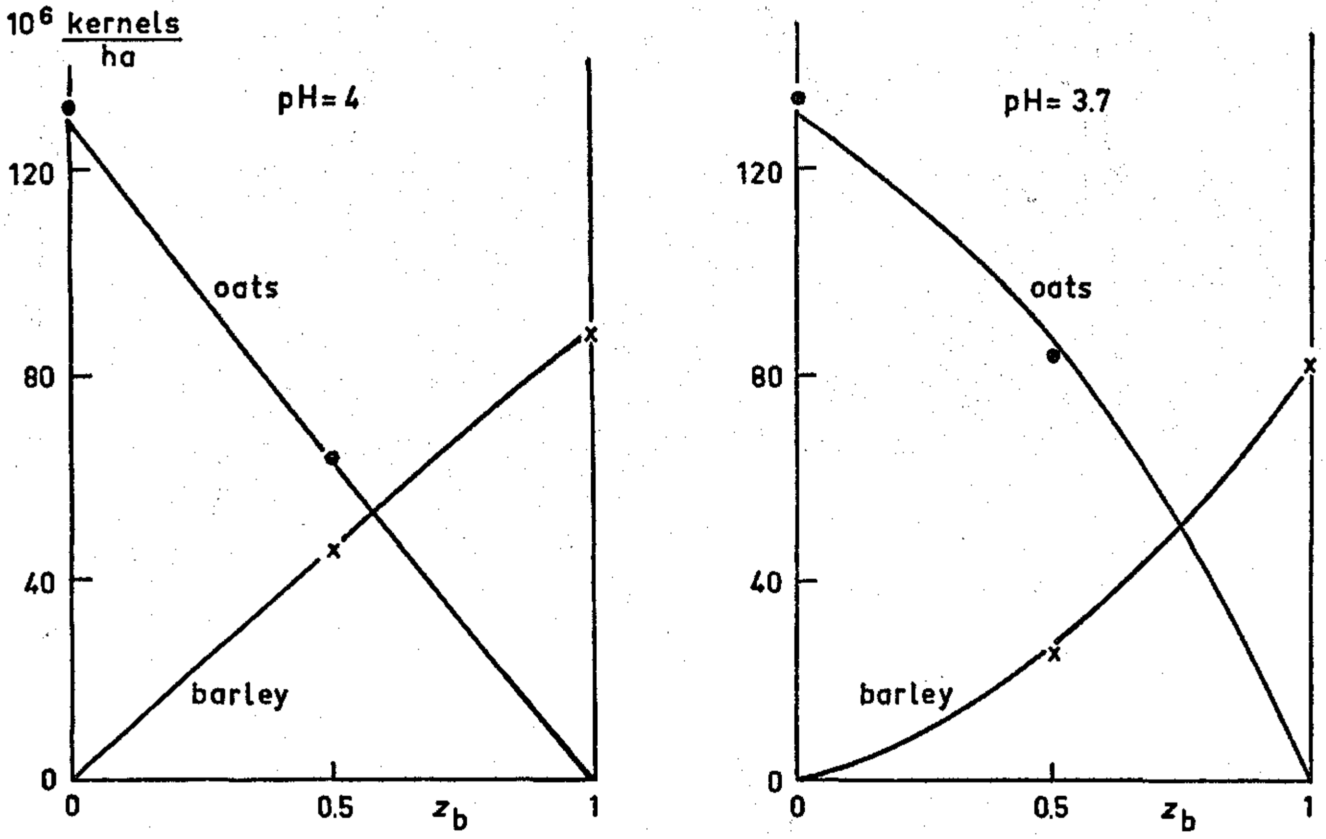

Figure 6. (Van Dobben, 1955; de Wit, 1960).

The pH-KCl, used here, is about one unit lower than the pH-H_2O.

Likewise, the yield depression of potatoes due to leafroll virus disease is also most pronounced when the leafroll diseased plants are grown in competition with healthy individuals (Figure 7).

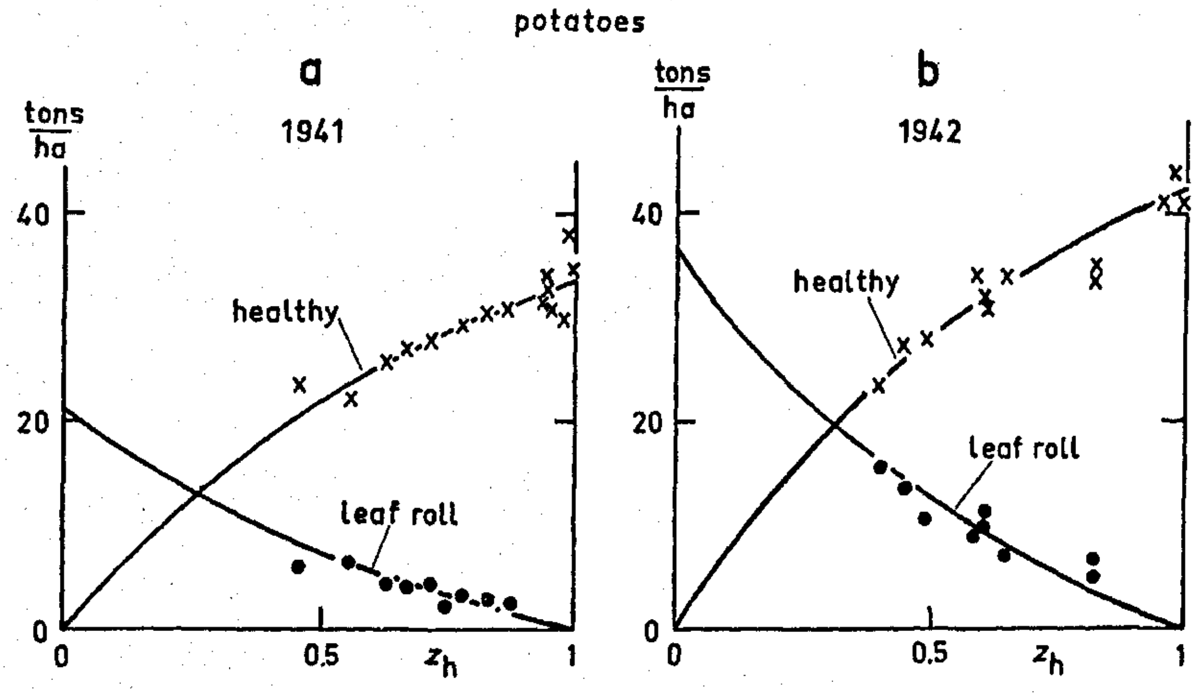

Figure 7. (Reestman, 1964; de Wit, 1960).

The impairment of growth due to nematodes, low pH and leafroll shows up in the curvature of the yield lines, because it is already effective before all space is claimed. This is not always the case, as shown in Figure 8 which represents the result of a replacement experiment with wheat of the Triticum durum and the T. vulgare species. The almost straight yield lines indicate that both species matched each other during the period that the space was claimed. However, a severe rust attack during the second part of the growing period made the T. vulgare suffer, but then it was too late for the T. durum to take over.

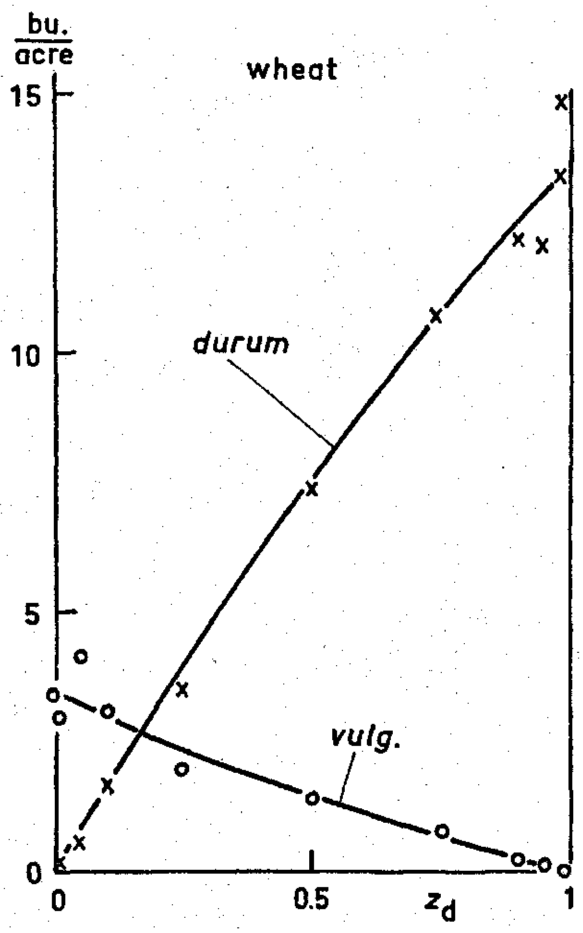

Figure 8. (Klages, 1936; de Wit, 1960).

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