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C. T. DE WIT

ON COMPETITION

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WAGENINGEN – THE NETHERLANDS

ON COMPETITION

C. T. DE WIT

CENTRUM VOOR
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CONTENTS

0. INTRODUCTION

> Het inrichten van experimenten op een zodanige wijze dat een wiskundige bewerking van de resultaten mogelijk wordt, het ontwerpen van speciale meetapparatuur daarvoor, het streven naar generalizeren van de verkregen uitkomsten en het met elkander in verband brengen van gebieden die uiterlijk verschillend zijn, doch die blijken in hun mathematische ondergrond overeenkomst te vertonen, dit zijn eigenaardigheden van de natuurkunde, waaraan zij haar praktische waarde ontleent ook voor die gebieden van de techniek en natuurwetenschap, die ver staan van de eigenlijke in de natuurkunde behandelde onderwerpen.[1]
>
> W. R. VAN WIJK: De natuurkunde in de wetenschap en in de techniek. Rede L.H.S., Wageningen (1948).

It appears that field experiments are of limited value for improving our knowledge concerning the conditions which govern the distribution and abundance of plant species in a permanent pasture.

The result of experiments in the field can hardly be treated quantitatively because many undeterminate factors are of importance. The effect of weather on the results is great. Moreover, there is hardly a good measure for the 'competitive power' of the species. Such a good measure can only be found with the aid of suitable experiments, but suitable experiments can only be designed if it is more or less known how the 'competitive power' of plants with respect to each other is measured.

In order to arrive at some useful characteristic for the 'competitive power', DE WIT and ENNIK (1958) studied experiments on competition between species which effect each other in a less complicated way than perennial grassland species. An analogy between competition phenomena and the theories underlying multicomponent distillation and other exchange processes was noted and on basis of this analogy a theory was developed which makes it possible to describe many competition phenomena quantitatively.

This theory has been worked out in detail and is represented in this paper up to the level where it is proved that the approach is suitable to interpret competition experiments with perennial (grassland) species.

The theory is of course in many ways connected with other theories which are often more or less independently developed in animal ecology, plant ecology and population genetics. The treatment runs also parallel with theories developed in the field of

[1] Designing experiments in such a way that a mathematical treatment of the results is possible, constructing measuring apparatus for this purpose, aiming at generalization of observational results and at relating fields of knowledge which are outwardly different but which appear to agree as far as their mathematical treatment goes, these are peculiarities of physics from which it derives its practical value, also for those fields of technics and natural science, which are foreign to the subjects proper of physics.

enzyme kinetics (DIXON and WEBB, 1958), ion exchange (BOYD, SCHUBERT and ADAMSON, 1947) and competitive uptake of ions (EPSTEIN and LEGGET, 1954). It was therefore possible to make good use of and to incorporate excisting theories in the present approach.

The paper is divided in ten main sections. A summary is given at the beginning of each main section.

The author is indebted to Dr. P. J. ZWERMAN (Cornell University, New York) for his critical remarks on a draft of this paper and to Ir. J. P. VAN DEN BERGH, Dr. W. H. VAN DOBBEN and Ir. G. C. ENNIK (I.B.S., Wageningen) for their cooperation.

I. THE SIMPLEST MODEL OF COMPETITION

1.0. SUMMARY

The simplest model of competition which can be imagined enables one to introduce some basic relations, terms and graphical representations in a convenient way. The practical value is limited, however, because the model is based on the assumption that the growth of an organism is not affected by its neighbours. Such peaceful coexistence excludes competition in the ordinary sense of the word.

In spite of this limitation, the model is used in population genetics, although it has met with more and more opposition during recent years. The reason for its being used in this branch of science is that it serves very well to illustrate the effect of natural selection which can take place without competition.

1.1. THE MODEL

1.1.1. *The basic assumptions*

Let us consider a homogeneous field plot of unit surface (i.e. ha) which is split up in squares by means of a marker, as illustrated in figure 1. Let us suppose, moreover, that a stock of seeds of species S_1 and of species S_2 is available and that on each square one seed, either of S_1 or of S_2 is planted and that at harvest the numbers of seeds of S_1 and S_2 are determined separately.

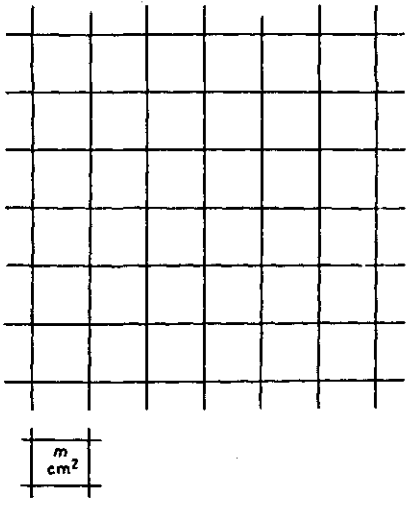


FIG. 1. A field divided in squares with a size of m cm², each planted with one seed.

The yields of species S_1 and S_2 are called O_1 and O_2 respectively, and expressed in numbers of seeds per unit surface; the sum of both $(O_1 + O_2)$ equals the total number of seeds harvested. A mono culture is obtained on fields which are planted with the seeds of one species. The symbols M_1 and M_2 are used for the yield per unit

surface of the monocultures of S_1 and S_2, respectively. The numbers of seeds planted of S_1 and S_2 are represented by Z_1 and Z_2, respectively. The total number of seeds $(Z_1 + Z_2)$ is equal to the total number of squares or the unit surface divided by m, the surface of one square. It is only dependent on the value of m, which is supposed to be constant.

It is assumed, moreover, that the growth of a plant in one of the squares of the field is not affected by the growth of plants in any other square, or in other words, that there is neither intraspecific nor interspecific competition.

1.1.2. *The yield of fields with mixed culture*

If A_1 is the area of the field available for species S_1 and A_2 the area available for species S_2, the following relations hold:

$$A_1 : A_2 = mZ_1 : mZ_2 = Z_1 : Z_2 \tag{1.1}$$

$$A_1 + A_2 = [Z_1 + Z_2]m = \text{unit surface} = 1 \text{ or}$$

$$A_1 = Z_1[Z_1 + Z_2]^{-1} \tag{1.2}$$

$$A_2 = Z_2[Z_1 + Z_2]^{-1}$$

The yields, being proportional with the area available for each species, are now:

$$O_1 = Z_1[Z_1 + Z_2]^{-1}M_1 = z_1M_1$$

$$O_2 = Z_2[Z_1 + Z_2]^{-1}M_2 = z_2M_2 \tag{1.3}$$

$$O_1 + O_2 = z_1M_1 + z_2M_2 = [M_1 - M_2]z_1 + M_2$$

The relative seed frequencies $z_1 = Z_1[Z_1 + Z_2]^{-1}$ and $z_2 = Z_2[Z_1 + Z_2]^{-1}$ range from 0 to 1 such that the sum of both is one.

This rather complicated formulation of a simple matter is chosen in order to facilitate the treatment of more complex models in other sections.

Both frequencies are represented along the horizontal axis of figure 2a and the yields in numbers of seeds per surface unit along the vertical axis. The relations between the yield O_1 and the frequency z_1 is represented by the straight line 1, between O_2 and $z_2 = (1 - z_1)$ by the straight line 2 and between $[O_1 + O_2]$ and z_1 by the straight line 3. These lines represent the formulae 1.3. for arbitrary values of M_1 and M_2.

1.1.3. *The relative reproductive rate*

The reproductive rate is defined as the ratio of the number of seeds harvested and the number of seeds sown, and for plant species S_1 and S_2 given by:

$$a_1 = O_1Z_1^{-1} = [Z_1 + Z_2]^{-1}M_1 \text{ and} \tag{1.4}$$

$$a_2 = O_2Z_2^{-1} = [Z_1 + Z_2]^{-1}M_2$$

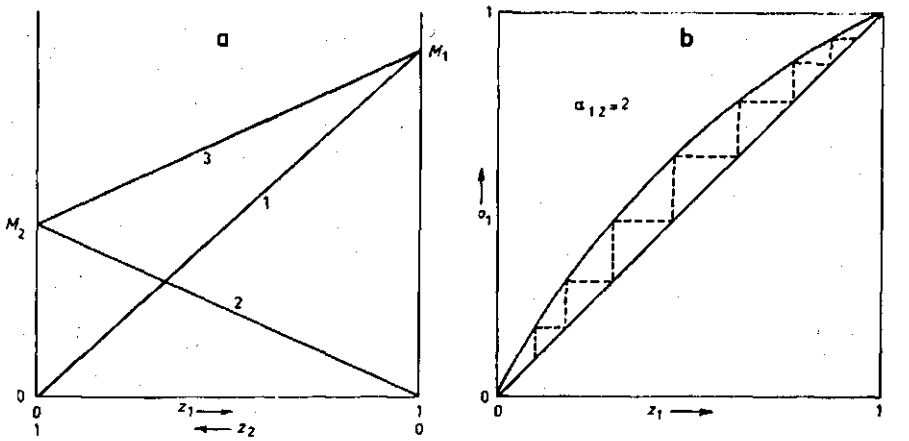


FIG. 2. a. A relation between the relative seed frequency and the yield of two species S_1 and S_2, 'coexisting peacefully'.
b. The frequency diagram, giving the relation between the relative frequency of species S_1 in the seed (z_1) and in the yield (o_1), as calculated from the lines of figure 2a.

As $Z_1 + Z_2$ is constant for a given value of m, the reproductive rates are constant, that is independent of the seed frequencies.

The relative reproductive rate of plant species S_1 growing with species S_2 on the same field is defined as:

$$\alpha_{12} = a_1 a_2^{-1} = M_1 M_2^{-1} \qquad 1.5$$

Of course this relative reproductive rate is also independent of the composition of the seed mixture. Instead of the term relative reproductive rate, the terms 'relative fitness', 'survival value' and 'adaptive value' are used for α in population genetics (LI, 1955).

1.1.4. *The frequency diagram and the ratio diagram*

Apparently

$$O_1 O_2^{-1} = \alpha_{12} Z_1 Z_2^{-1} \text{ or } o_1 o_2^{-1} = \alpha_{12} z_1 z_2^{-1} \qquad 1.6$$

in which

$$o_1 = O_1[O_1 + O_2]^{-1} \text{ and } o_2 = O_2[O_1 + O_2]^{-1}$$

or the ratio of the number of kernels in the harvest is equal to the relative reproductive rate times the ratio of the number of kernels in the original seed.

A part of the harvested seed may be sown again next year under the same conditions. The composition of the yield in this next year is of course equal to $\alpha_{12}^2 z_1 z_2^{-1}$. Repeating the experiment during n years under the same conditions a yield of the composition

$$[O_1 O_2^{-1}]_n = \alpha_{12}^n Z_1 Z_2 \text{ or } [o_1 o_2^{-1}]_n = \alpha_{12}^n z_1 z_2^{-1} \qquad 1.7$$

is obtained.

The number of generations necessary to obtain a certain change of the frequency of the seeds is easily estimated by means of a frequency diagram in which along the

horizontal axis the frequency z_1 and along the vertical axis the frequency o_1 is given.

This diagram, calculated from the data in figure 2a is given in figure 2b. The number of generations necessary to obtain from a mixture containing 10 percent of species S_1 ($z_1 = 0.1$) a mixture which contains at least 90 percent of species S_1 ($z_1 = 0.9$) is obtained by counting the steps in the broken line in figure 2b. Ten percent of species S_1 in the seed mixture yields 18 percent of species S_1 in the harvest mixture. Sowing again next year, a yield with 30 percent of species S_1 in the harvest mixture is obtained and so on. In this case seven generations are necessary to obtain a mixture which contains at least 90 percent of species S_1 from a mixture which contained only 10 percent.

An experiment in one year with mixtures ranging with relative seed frequencies from 0–1 gives full information on the change of composition of the mixture in n years, should it be possible to carry out an experiment during n years under exactly the same conditions.

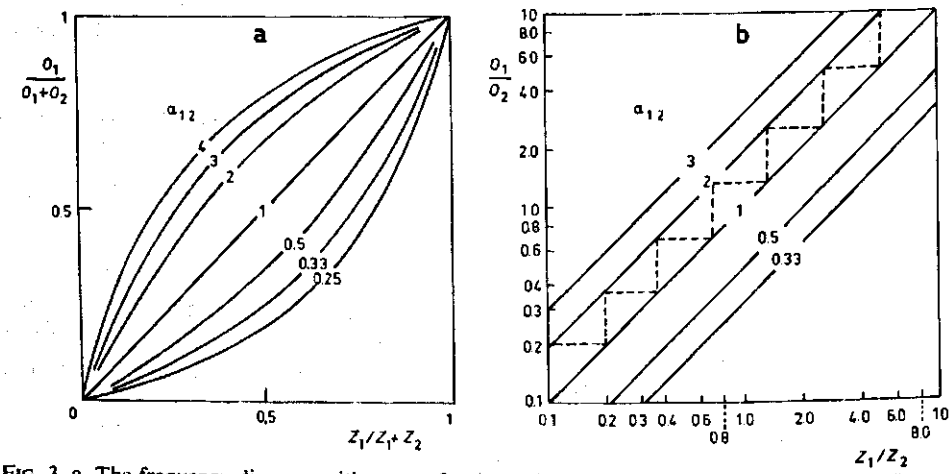


FIG. 3. a. The frequency diagram with curves for α ranging from 0.25 to 4.
b. The ratio diagram with lines for α ranging from 0.33 to 3.

The shape of the curves in the frequency diagram for values of α ranging from 0.25 to 4 is given in figure 3a. For α equal to one the curve is represented by the diagonal line, for α larger than one the curves are found above this line and for α smaller than one below this line. The curves are of course symmetrical with respect to the diagonal joining the points (0.1) and (1.0). It is evident that $\alpha_{12} = \alpha_{21}^{-1}$ or that the relative reproductive rate of species S_1 in a mixture of S_1 and S_2 is the inverse of the relative reproductive rate of species S_2 in a mixture of S_1 and S_2.

Equation 1.6 for the relative reproductive rate may be written as follows

$$\lg O_1 O_2^{-1} = \lg \alpha_{12} + \lg Z_1 Z_2^{-1} \qquad 1.8$$

so that the relation between the yield ratio and seed ratio can be presented on logarithmic paper by a straight line with a slope of 45 degrees. These lines for $\alpha = 3, 2, 1, \frac{1}{2}$ and $\frac{1}{3}$ are given in the ratio diagram of figure 3b.

The number of generations necessary to obtain a certain change of the ratio can be determined again by counting the steps in the broken line in the figure.

1.2. FISHER'S THEOREM OF NATURAL SELECTION

The average reproductive rate of the mixture is equal to

$$\bar{a} = [O_1 + O_2]\,[Z_1 + Z_2]^{-1} = \{[M_1 - M_2]z_1 + M_2\}\,[Z_1 + Z_2]^{-1} = \\ = m\{[M_1 - M_2]z_1 + M_2\}$$

The average reproductive rate of the mixture increases with increasing z_1 if M_1 is larger than M_2. On the other hand, if M_1 is larger than M_2, the relative reproductive rate of species S_1 is larger than one (formula 1.5) so that z_1 increases in course of time. Consequently the average reproductive rate of the mixture of the following generation is always larger than of the preceding generation until the species with the highest reproductive rate is left over.

FISHER (1930) formulated this conclusion quantitatively in a theorem which is known as the *Fundamental Theorem of Natural Selection.*

Suppose there are n species S_j ($j = 1; 2 \ldots; r$) in a mixture which do not interbreed. The relative frequency and the reproductive rate of species S_j are z_j and a_j respectively.

The mean and variance of the reproductive rate of the mixture are:

$$\bar{a} = \Sigma z_j a_j \; ; \quad \sigma_a^2 = \Sigma z_j [a_j - \bar{a}]^2 = \Sigma z_j a_j^2 - \bar{a}^2$$

The relative frequency o_j of the species S_j in the harvest is $z_j a_j$ and, because a_j is supposed to be independent of z_j, with a reproductive rate of a_j.

Hence the new average reproductive rate becomes

$$\bar{a}' = [\Sigma o_j a_j]\,[\Sigma o_j]^{-1} = [\Sigma z_j a_j^2]\bar{a}^{-1}$$

and the gain in average reproductive rate due to cultivation during one year is

$$\Delta\bar{a} = \bar{a}' - \bar{a} = [\Sigma z_j a_j^2]\bar{a}^{-1} - \bar{a} = \sigma_a^2 \bar{a}^{-1} > 0 \qquad 1.9$$

Or in words: the rate of increase of the reproductive rate of a mixture in any year is equal to the variance of the reproductive rate in that year. Which is a quantitative formulation of Fisher's Fundamental Theorem of Natural Selection. This theorem can only be proved under the assumption that the reproductive rate of a species is a constant.

1.3. THE PRACTICAL VALUE OF THE MODEL

Experiments with crop mixtures, sown at normal densities, which proved that the model discussed in this section is of any practical value have not been found. Plants do not restrict themselves in general to the arbitrary surface allotted to them and effect

the growth of plants in neighbouring squares. This simple model appears to hold only under conditions where the surface of the squares in figure 1 are large compared with the size of the plants (i.e. where there is no competition for space) or where 'the competitive forces' of the two plant species balance each other (see section 3).

As far as population genetics is concerned, this model is nevertheless of some value because it proves that natural selection is possible under conditions where there is no competition. It may account under these conditions at least for the quantitative effect of natural selection on the relative gene frequencies within a population.

2. AN ANALOGY WITH BINARY MIXTURES OF LIQUIDS

2.0. SUMMARY

The relations between the composition of the vapour and liquid phase in case of solutions of liquids in liquids are discussed, because the treatment of these relations are used as a model for the treatment of the relations between the composition of crop mixtures in a first and second generation.

2.1. RAOULT'S LAW

Two liquids like benzene and toluene may be mixed in all proportions. Raoult's law states now that at constant temperature the partial vapour pressure of benzene and of toluene above a vessel with a mixture of both liquids is proportional with the molar fractions of both substances in the liquid (see for instance PERRY, 1951; MEE, 1958).

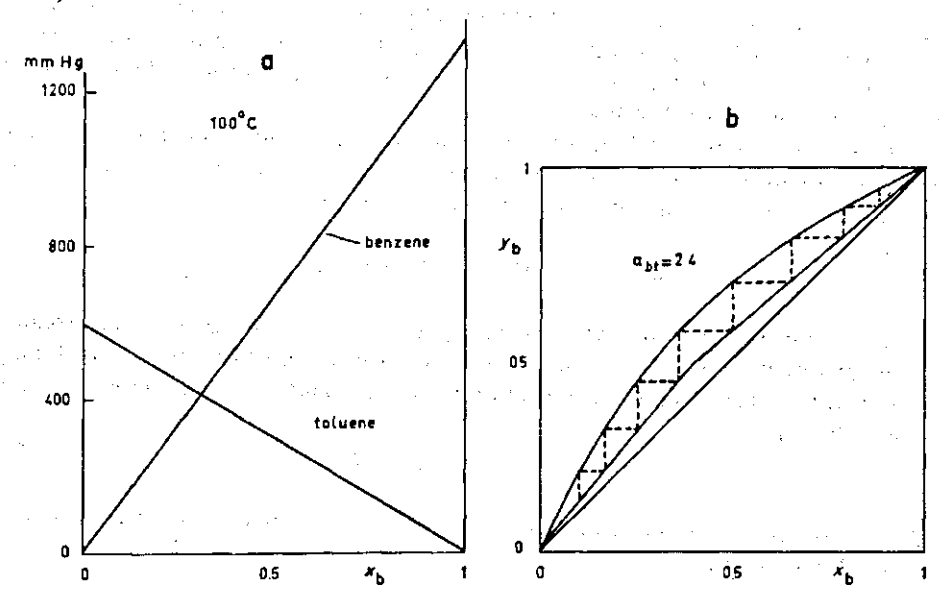


FIG. 4. a. The relation between the vapour pressure in mm Hg of benzene and toluene and the molar composition (x_b) of the liquid phase at 100° C.
b. The relation between the molar composition of a mixture of benzene and toluene in the vapour (y_b) and liquid (x_b) phase at 100° C.

This relation is graphically represented in figure 4a. The mole fraction of benzene (x_b) in the liquid is placed along the horizontal axis. The mole fraction of toluene (x_t) is of course equal to one minus the mole fraction of benzene. The partial vapour

pressure of benzene (Y_b) and toluene (Y_t) are given now by the lines. The molar fractions in the liquid are of course analogous with the relative number of seeds in the sown mixture, and the partial vapour pressures with the yields in figure 2.

Apparently the relation

$$Y_b : Y_t = x_b P_b : x_t P_t \qquad 2.1$$

holds in which P_b and P_t are the partial vapour pressures above pure liquids of benzene and toluene; which are at a temperature of 100° C equal 1344 and 559 mm Hg, respectively. The relative volatility is defined as

$$\alpha_{bt} = [Y_b x_b^{-1}]\,[Y_t x_t^{-1}]^{-1} = P_b P_t^{-1} \qquad 2.2$$

which is in this case equal to $1344/559 = 2.4$. The relative volatility is analogous with the relative reproductive rate in the biological model.

A graphical representation is given in figure 4b. The mole fraction of one component in the liquid (x_b) is given along the horizontal axis and in the vapour $y_b = Y_b[Y_b + Y_t]^{-1}$ along the vertical axis. This diagram is analogous with our frequency diagram of figure 2b. The number of plates of a distillation column (which is a measure for its 'length') necessary to obtain a certain change of composition is counted in the same way as in our model the generations are counted. Due to the nature of the process of distillation, the 'reference line' is not the 45 degree line as in the biological model (figure 2b), but another set of lines.

RAOULT's law appears to hold only for what are called ideal mixtures, that are mixtures of homologous series, isomers, and so on. This is again in analogy with the biological model which holds if there is no competition.

2.2. ACTIVITY COEFFICIENTS

There are many mixtures for which Raoult's law does not hold. They are treated with the introduction of activity coefficients (see for instance PERRY, 1951), which may supposed to be experimental multiplication factors (γ_1 and γ_2) chosen in such a way that the relation

$$Y_1 : Y_2 = \gamma_1 x_1 P_1 : \gamma_2 x_2 P_2 \qquad 2.3$$

holds for mixtures of a liquid L_1 and L_2, instead of the simple relation (2.1). The relative volatility is then equal to

$$\alpha_{12} = [Y_1 x_1^{-1}]\,[Y_2 x_2^{-1}]^{-1} = [\gamma_1 P_1]\,[\gamma_2 P_2]^{-1} \qquad 2.4$$

It appears that within a certain range, which may be large or small the activity coefficients or their quotients are practically constant and that for a mixture of n components it is convenient to work with the following relation:

$$Y_1 : Y_2 : \ldots : Y_i : \ldots : Y_n = \gamma_1 x_1 P_1 : \gamma_2 x_2 P_2 : \ldots : \gamma_i x_i P_i : \ldots : \gamma_n x_n P_n \qquad 2.5$$

The relative volatilities with respect to an arbitrary reference component are

$$\alpha_{1i} = [\gamma_1 P_1]\,[\gamma_i P_i]^{-1};\ \alpha_{ii} = [\gamma_i P_i]\,[\gamma_i P_i]^{-1} = 1;\ \alpha_{ni} = [\gamma_n P_n]\,[\gamma_i P_i]^{-1} \qquad 2.6$$

The relative volatility of the reference component is than of course equal to one and the relation

$$\alpha_{kj} = \alpha_{ki}\,\alpha_{ji}^{-1} \qquad 2.7$$

holds. This approach proves to be very convenient in multicomponent distillation.

Similar coefficients will be introduced in the next section and it will be proved in this paper that the use of these enables a quantitative treatment of competition problems.

2.3. Diagrams of vapour composition versus liquid composition

The 'frequency diagrams' holding for a mixture following Raoult's law or for a mixture with at least a constant relative volatility are as given in the diagram of figure 4b or of figure 3a. The shape of the curves is much more complex if the components of a mixture affects each other in such a way that the relative volatility is not constant. In such cases curves like those in the diagram of figure 5 may be obtained.

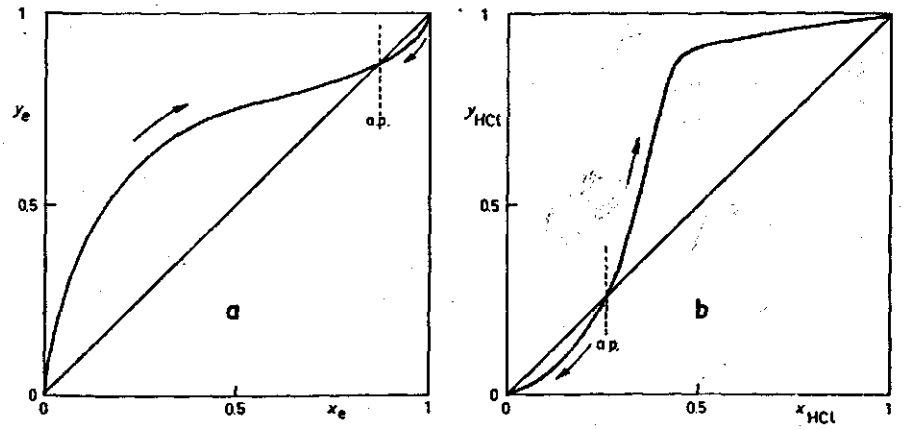


FIG. 5. a. The relation between the molar composition of a mixture of ethanol and water in the vapour (y_b) and liquid (x_b) phase at an arbitrary pressure.
b. The same for a mixture of HCl and water.

Diagram 5a represents the relation between the vapour composition and the liquid composition of a mixture of ethanol and water at an arbitrary pressure. The curve crosses the 45 degrees line. At this point, the azeotropic point, no enrichment of the vapour is obtained. The composition of a mixture during distillation changes in the direction of the arrows. Whatever the starting composition, a mixture is obtained which contains about 90 percent ethanol and 10 percent water. The equilibrium at the azeotropic point is in this case a stable one.

Diagram 5b represents the relation between the composition of the vapour and the composition of the liquid of a mixture of HCl and water at an arbitrary pressure. There is again an azeotropic point. The composition of the mixture changes during distillation in the direction of the arrows. The equilibrium is here unstable: depending on the starting composition, the fraction HCl in the mixture increases or decreases during distillation.

It will be shown that similar 'azeotropic points' may occur in mixtures of plant species.

3. CROWDING FOR THE SAME SPACE WITHIN BARLEY-OATS MIXTURES

3.0. SUMMARY

A crowding coefficient analogous with the activity coefficients of liquids in a mixture is introduced in this section and a model describing the competition within mixtures of barley and oats is developed. This model is of use in any case where two organisms crowd for the same space, but do not affect each other in any other way. Practical conclusions with respect to mixed cultivation of barley and oats and with respect to population dynamics will be arrived at.

3.1. THE EXPERIMENTS

The Agricultural Extension Service of the Dutch Government executed during the years 1951–1954 about 33 field experiments on sandy soils concerning mixed cultivation of barley *(Hordeum vulgare)* and oats *(Avena sativa)* under the direction of VAN DOBBEN. Results were published by VAN DOBBEN (1951, 1952, 1953). The original data used in this paper were extracted from files of the Institute for Biological and Chemical Research on Field Crops and Herbage at Wageningen.

The experiments were of the following design. Mixtures of barley and oats were sown at normal rate, but such that the number of seeds per hectare was the same for any mixture. The number of barley seeds in the mixture expressed as a fraction of the total number were 0, $\frac{1}{3}$, $\frac{1}{2}$, $\frac{2}{3}$ and 1, the number of oats seeds as a fraction of the total were 1, $\frac{2}{3}$, $\frac{1}{2}$, $\frac{1}{3}$ and 0 in the same order.

At harvest, the seed weights of barley and oats were determined separately. Thousand kernel weights of the harvested barley and oats were also determined, so that it is possible to calculate the number of harvested kernels of each species on each plot. The data in this section concern the yield in number of kernels per surface unit and, except were otherwise stated, not the kernel weight per surface unit. The unit 'a million of kernels per hectare' is abbreviated as '10^6 kernels ha^{-1}'.

The results of experiment MB 22-1952 are represented in figure 6a. Along the horizontal axis the frequency of the barley and oats kernels in the seed mixture, represented by the symbols z_b and z_o respectively, are given. The sum of both is always one. The yields of barley and oats expressed in numbers of kernels per hectare are represented by crosses and dots. The yield of barley and oats which is to be expected under the assumption that the simple model of section 1 is valid is represented by the straight lines 1 and 2, respectively.

It appears that the yields of barley are smaller and of oats higher than the expected yields. Inspection of the results of the 33 experiments revealed that in all cases one of the species yielded more and the other yielded less than expected according the simple model of section 1. This suggests that one species crowded the other out of the space allotted according to the composition of the sown mixture.

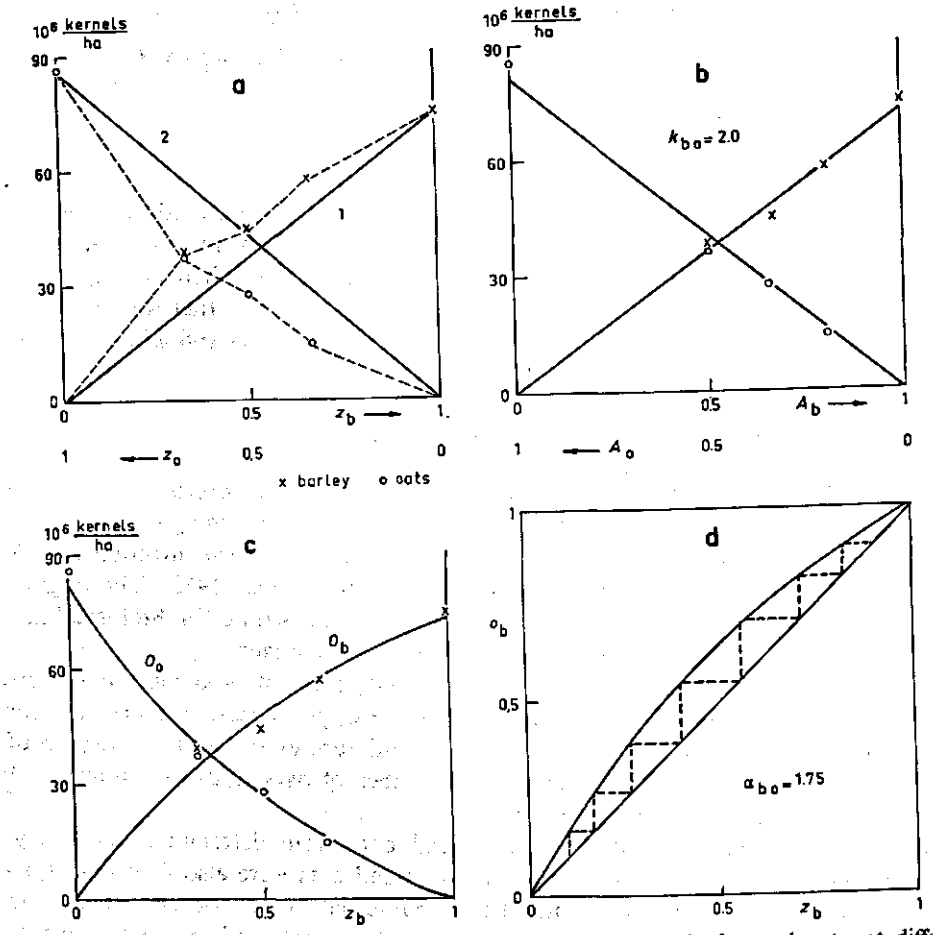


FIG. 6. The result of competition experiment MB 22–1952 between barley and oats, at different relative seed rates, the absolute seed rate or the space per seed (m) being kept constant. Data from VAN DOBBEN (1953).

3.2. A MODEL OF CROWDING FOR THE SAME SPACE

The homogeneous field plot represented in figure 1 is again considered and the same symbols as in section 1.1. are used to represent the numbers of seeds, the yields of mixed culture and mono culture and so on. The total number of seeds per unit surface, is again given by

$$Z_1 + Z_2 = m^{-1} \qquad 3.1a$$

Instead of the basic assumptions of equation 1.1, i.e.

$$A_1 : A_2 = Z_1 : Z_2 \qquad 1.1$$

$$A_1 + A_2 = 1$$

it is supposed that for the space with species S_1 and S_2, A_1 and A_2 respectively, the following relation hold:

$$A_1 : A_2 = b_1 Z_1 : b_2 Z_2$$
$$A_1 + A_2 = \text{a constant} = 1 \qquad 3.2$$

The multiplication factors b_1 and b_2 are analogous with the activity coefficients of binary mixtures and called crowding coefficients. The right hand side of equation 3.2 can be multiplied by an arbitrary chosen constant which means that only the quotient $k_{12} = b_1 b_2^{-1}$ is determinate. The number k_{12} is called the relative crowding coefficient of species S_1 with respect to species S_2.

The equations are a mathematical expression of the statement that the two plant species affect each other only by crowding for the same space, and of course only of practical value under conditions where the relative crowding coefficient appears independent of the relative seed frequency.

Although the crowding coefficient is formally equal to the activity coefficient, there is a large difference. Activity coefficients as used in distillation characterize a dynamical equilibrium, whereas the crowding coefficient characterize not the process of crowding itself, but only the result of this crowding. This difference appears to be of great importance at a later stage (section 8.4.), where the results of experiments at different spacings (values of m) are considered.

The condition that $A_1 + A_2$ is one or constant implies that the two plant species which compete for the same space exclude each other. This space is not defined at present in terms with a physiological meaning, because this is not necessary for a quantitative description of the phenomena. One may read for the term space 'growing factors', or 'requisites' like water, minerals, light and so on which are homogeneously distributed over and in the field where the plants grow. Such a description is, however, not necessary, always inaccurate and therefore unadvisable.

It follows from equation 3.2 that

$$\begin{aligned} A_1 &= b_1 Z_1 [b_1 Z_1 + b_2 Z_2]^{-1} = k_{12} Z_1 [k_{12} Z_1 + Z_2]^{-1} \\ A_2 &= b_2 Z_2 [b_1 Z_1 + b_2 Z_2]^{-1} = \quad Z_2 [k_{12} Z_1 + Z_2]^{-1} \end{aligned} \qquad 3.3$$

so that, M_1 and M_2 being again the yields of the mono cultures, the yields of the two species S_1 and S_2 are to be represented by the following equations.

$$O_1 = b_1 Z_1 [b_1 Z_1 + b_2 Z_2]^{-1} M_1 \text{ and } O_2 = b_2 Z_2 [b_1 Z_1 + b_2 Z_2]^{-1} M_2 \qquad 3.4a$$

The relative seed frequencies of the species are defined by

$$z_1 = Z_1 [Z_1 + Z_2]^{-1} \text{ and } z_2 = Z_2 [Z_1 + Z_2]^{-1} \qquad 3.5a$$

so that the equations may be written also in the following form

$$\begin{aligned} O_1 &= k_{12} z_1 [k_{12} z_1 + z_2]^{-1} M_1 = k_{12} z_1 \{[k_{12} - 1] z_1 + 1\}^{-1} M_1 \\ O_2 &= \quad z_2 [k_{12} z_1 + z_2]^{-1} M_2 = k_{21} z_2 \{[k_{21} - 1] z_2 + 1\}^{-1} M_2 \end{aligned} \qquad 3.4b$$

with $k_{12} = k_{21}^{-1}$.

A similar set of equations hold if in each square of m cm^2 either c_1^{-1} seeds of species S_1 or c_2^{-1} seeds of species S_2 are placed so that

$$c_1 Z_1 + c_2 Z_2 = m^{-1} \qquad 3.1b$$

These factors c are most conveniently treated by defining the relative seed frequencies by

$$z_1 = c_1 Z_1 [c_1 Z_1 + c_2 Z_2]^{-1} \text{ and } z_2 = c_2 Z_2 [c_1 Z_1 + c_2 Z_2]^{-1} \qquad 3.5b$$

or eliminated by expressing seed and harvest rates in seed and harvest units which are c_1^{-1} or c_2^{-1} times the original values.

The reproductive rates of species S_1 and S_2 are

$$\begin{aligned} a_1 &= O_1 Z_1^{-1} = m k_{12} [k_{12} z_1 + z_2]^{-1} M_1 \\ a_2 &= O_2 Z_2^{-1} = m \quad [k_{12} z_1 + z_2]^{-1} M_2 \end{aligned} \qquad 3.6$$

The reproductive rates of *both* species increase with increasing z_1 (and decreasing z_2) if the relative crowding coefficient k_{12} is smaller than one. The reproductive rates decrease with increasing z_1 if k_{12} is larger than one. The reproductive rates are not constant.

The relative reproductive rate of species S_1 in a mixture of both species is equal to

$$\alpha_{12} = [O_1 Z_1^{-1}] [O_2 Z_2^{-1}]^{-1} = k_{12} M_1 M_2^{-1} \qquad 3.7a$$

or

$$\alpha_{12} = [O_1 Z_1^{-1}] [O_2 Z_2^{-1}]^{-1} = c_1 c_2^{-1} k_{12} M_1 M_2^{-1} \qquad 3.7b$$

if the factors c are not eliminated.

The denominator of the reproductive rates, containing the variables z cancels, so that it appears that the relative reproductive rate is independent of z_1 and z_2 or the composition of the seed mixture.

3.3. The treatment of the results of field experiments

The equations (3.4b) and (3.7a) are rewritten in the following form

$$O_b = k_{bo} z_b [k_{bo} z_b + z_o]^{-1} M_b \text{ and } O_o = z_o [k_{bo} z_b + z_o]^{-1} M_o \qquad 3.4b$$

$$\alpha_{bo} = [O_b Z_b^{-1}] [O_o Z_o^{-1}]^{-1} = k_{bo} M_b M_o^{-1} \qquad 3.7a$$

in which the indices b and o refer to barley and oats, respectively. The equations contain one independent variable $z_b (z_o = 1 - z_b)$ and three constants M_b, M_o and k_{bo} which depend on the growing conditions and are not the same for different experimental fields.

A rough estimate of the value of the relative crowding coefficient k_{bo} may be obtained as follows. The yields of barley and oats at z_b values of 0.33, 0.50 and 0.67

furnish three independent estimates of the relative reproductive rates. By substituting the experimental values for M_b and M_o in equation 3.7a three dependent and inefficient estimates of k_{bo} are obtained, which may be averaged.

The following trial and error method is adopted to obtain more reasonable estimates for all the three constants M_b, M_o and k_{bo}. The constant k_{bo} is estimated as described above. This estimated value is substituted in the equations

$$A_b = k_{bo}z_b[k_{bo}z_b + z_o]^{-1} \text{ and } A_o = z_o[k_{bo}z_b + z_o]^{-1}$$

and the values of A_b and A_o for z_b equal to 0.33, 0.50 and 0.67 are calculated. Subsequently the yield data of barley and oats are represented in a graph with along the horizontal axis A_b $(0 \rightarrow 1)$ and A_o $(1 \rightarrow 0)$ and along the vertical axis the yields. The yield data for oats and barley, *both*, are to be found around a straight line, if the equations are applicable and the estimated value of k_{bo} is correct. If this is not the case slightly other values are tried until this is the case. It must be kept in mind that the barley and oat yields of the fields with a mixed crop are subject to partly the same errors.

The final result for experiment MB 22-1952 is given in figure 6b. It appears that $M_b = 72 \times 10^6$ kernels ha^{-1}, $M_o = 82 \times 10^6$ kernels ha^{-1} and $k_{bo} = 2.0$. Subsequently, smoothed curves are drawn in the original graphs by means of the equations

$$O_b = 2.0z_b[2.0z_b + z_o]^{-1}\ 72 \times 10^6 \text{ kernels per ha}$$

$$O_o = \quad z_o[2.0z_b + z_o]^{-1}\ 82 \times 10^6 \text{ kernels per ha}$$

These curves together with the observations are represented in figure 6c.

The estimated value of the relative reproductive rate α_{bo} appears to be $2.0 \times 72 \times 82^{-1} = 1.75$. The frequency diagram, calculated by means of this value is given in figure 6d.

The results of the 32 other experiments are reproduced in the graphs 1–32 of figure 7. The curves satisfy the equations 3.4b. The relative crowding coefficient, the relative reproductive rate and the pH and the registration number of the experiments, which were all carried out on sandy soils are given in the caption of the figure. Apart from some large deviations, the observations are close to the calculated curves.

3.4. The Montgomery effect

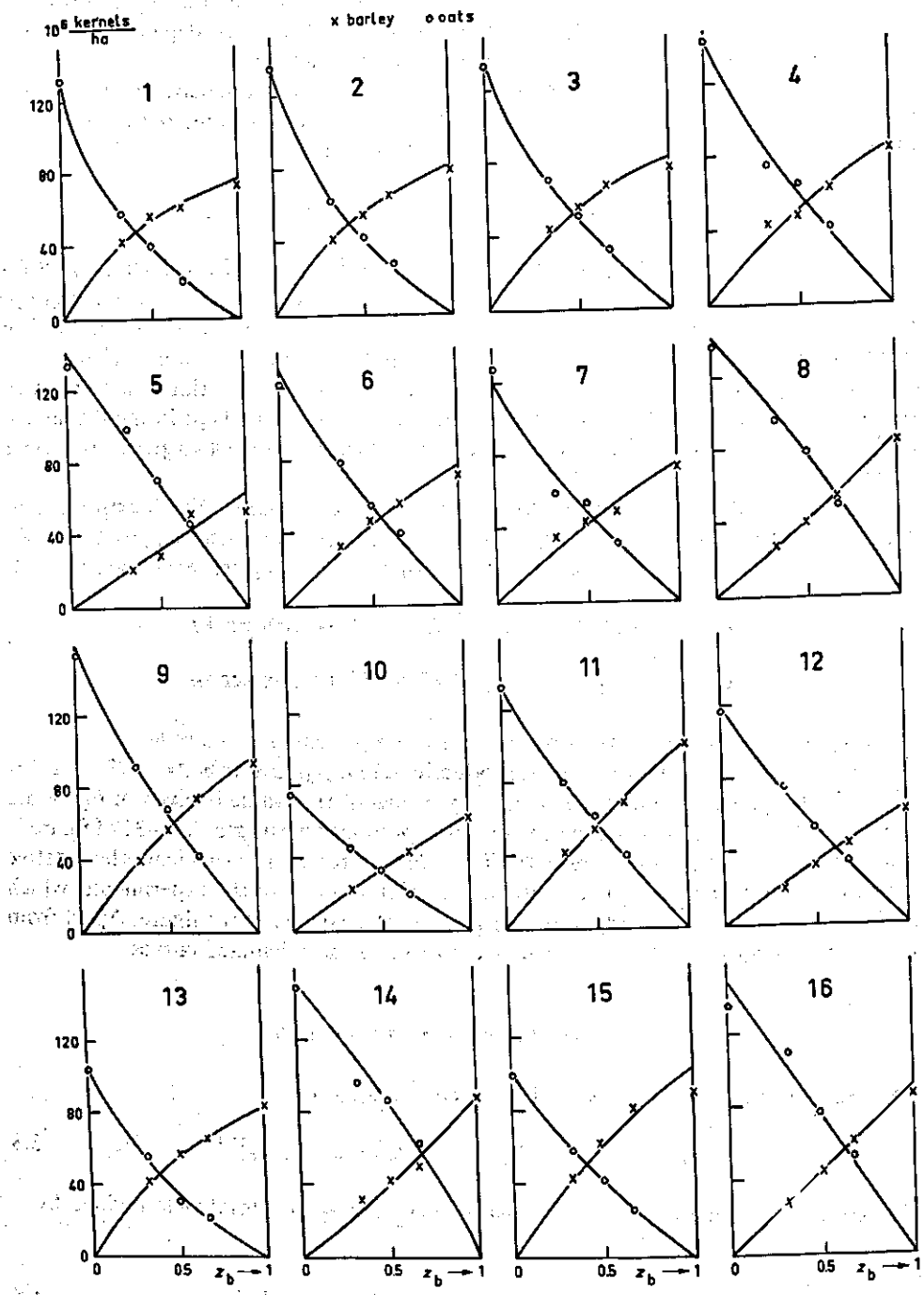
The total yield in number of kernels is of course equal to

$$O_b + O_o = [M_b k_{bo} z_b + M_o z_o]\ [k_{bo}z_b + z_o]^{-1} \qquad 3.8$$

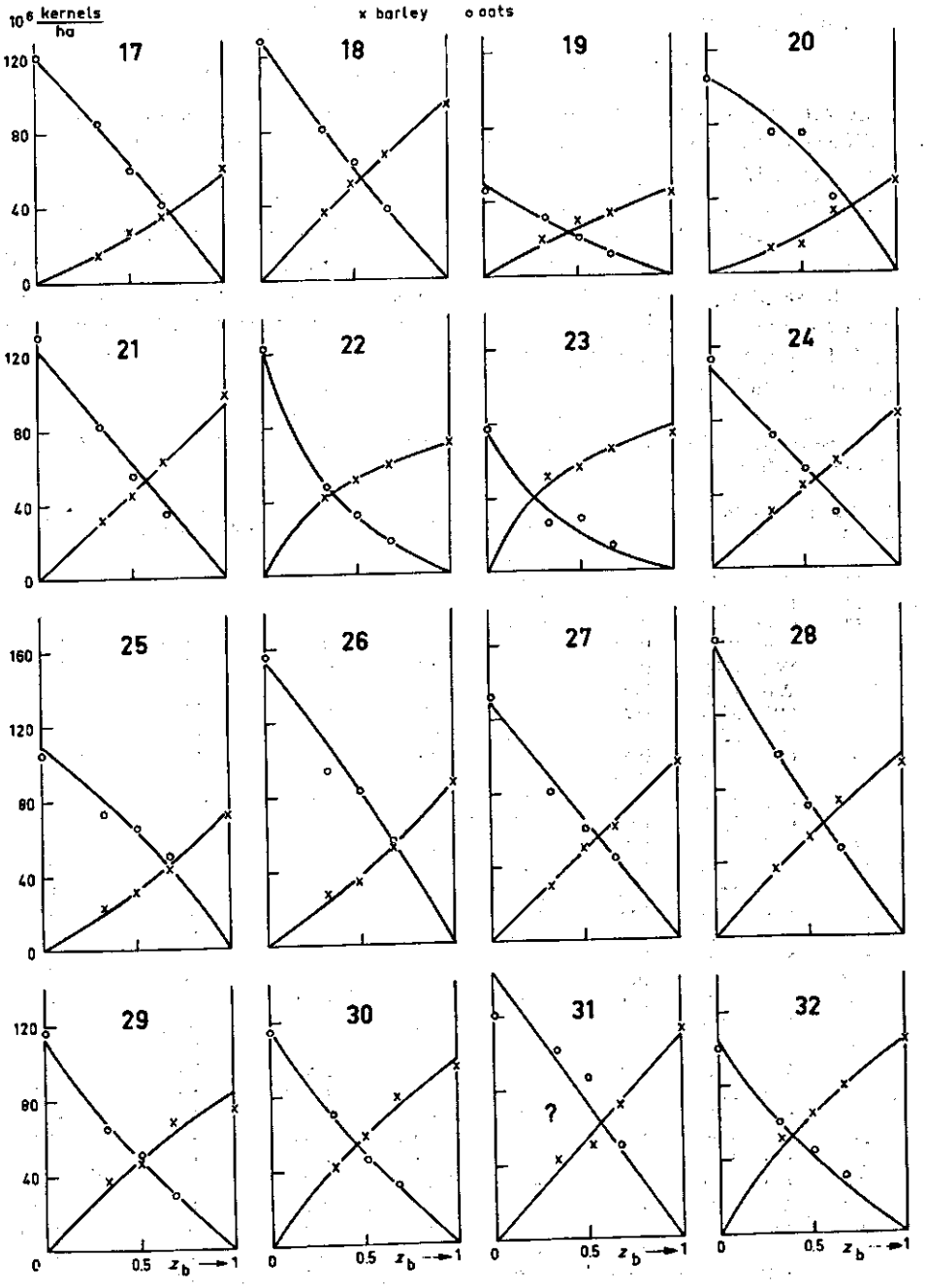
The average reproductive rate of the mixture is equal to this total yield divided by

$m^{-1} = Z_b + Z_o$ or

$$\bar{a} = m[M_b k_{bo} z_b + M_o z_o]\ [k_{bo}z_b + z_o]^{-1} \qquad 3.9$$



Caption on page 20



Caption on page 20

The increase or decrease of this reproductive rate with varying z_b can be found by differentiating $\bar{a}$ with respect to z_b. The result appears to be

$$d\bar{a}(dz_b)^{-1} = mk_{bo}[M_b - M_o]\,[(k_{bo} - 1)z_b + 1]^{-2} \qquad 3.10$$

The average reproductive rate increases (decreases) with increasing z_b if the sign of this differential quotient is positive (negative). This sign depends only on the sign of the difference $[M_b - M_o]$.

As for the experiment of figure 6, M_o appears to be larger than M_b. The average reproductive rate of the mixture decreases therefore with increasing z_b. On the other hand, α_{bo} is larger than one so that z_b increases if the mixture is resown repeatedly under the same conditions. The average reproductive rate of the mixture decreases therefore under the conditions of this experiment. The Fundamental Theorem of Natural Selection as formulated by FISHER (section 1.2.) does therefore not and not even qualitatively, hold in this case.

FIG. 7. The result of 32 competition experiment of barley and oats. Data from VAN DOBBEN (1951, 1952, 1953 and files).

Number graph.	Number exp.	Year	pH (KCl)[1]	k_{bo}	α_{bo}	M_b 10^6 kernels/ha	M_o 10^6 kernels/ha
1*	W 1326	1951	6.40	2.6	1.49	76	133
2*	PO 415	1951	5.50	2.2	1.32	82	137
3*	O.O 1396	1951	6.05	1.9	1.13	84	141
4	WB 1908	1951	5.60	1.4	0.82	86	146
5	WB 1909	1951	5.45	1.0	0.45	63	141
6	WB 1910	1951	5.75	1.4	0.82	76	130
7	OB 3241	1951	5.50	1.2	0.80	78	117
8	OB 3242	1951	5.70	0.83	0.51	87	142
9	CI 1127	1951	5.90	1.4	0.86	96	157
10	U 735	1951	5.70	1.2	0.96	61	76
11	OB 3283	1952	4.80	1.2	0.91	101	133
12	OB 3284	1952	4.30	1.2	0.65	64	119
13*	MB 23	1952	4.70	2.0	1.61	83	103
14	MB 24	1952	4.05	0.83	0.49	89	151
15*	O.O 1420	1952	5.45	1.4	1.41	102	101
16	O.O 1421	1952	4.95	1.0	0.61	90	148
17	WD 172	1952	3.90	0.83	0.41	58	118
18	WD 173	1952	4.40	1.2	0.87	96	132
19*	U 792	1952	4.80	1.4	1.29	46	50
20	U 793	1952	4.50	0.62	0.31	52	106
21	U 794	1952	5.75	1.0	0.77	95	123
22*	U 825	1953	4.90	3.0	1.71	69	121
23*	U 826	1953	5.40	3.0	3.04	78	77
24	OB 3332	1953	5.05	1.0	0.80	87	109
25	OF 959	1953	4.50	0.72	0.50	75	107
26	O.O 1469	1953	3.90	0.83	0.47	85	152
27	O.O 1470	1953	4.25	1.0	0.74	96	129
28	O.O 1540	1954	4.80	1.2	0.73	98	161
29*	WD 251	1954	5.50	1.4	1.04	84	113
30*	O.O 1541	1954	5.00	1.4	1.16	98	118
31	U 860	1954	4.60	1.0	0.76	109	143
32*	OB 3379	1954	4.60	1.6	1.55	104	107

[1] See note on page 23.

It is obvious that the average reproductive rate of the mixture decreases always in course of time if the growing conditions are such that

$$M_b < M_o \text{ and } k_{bo} > M_o M_b^{-1}$$

or

$$M_b < M_o \text{ and } \alpha_{bo} > 1 \qquad 3.11$$

It appears that $M_b < M_o$ for all 33 experiments. In spite of this α_{bo} is greater than one in 11 out of 33 experiments. These experiments are marked with a cross (*) in the caption of figure 7.

GUSTAFSSON (1951) collected examples of experiments in which the species or variety yielding best alone did not survive, when repeatedly sown in competition with an other species or variety. These experiments cannot be treated quantitatively because the growing conditions and consequently the constants governing the outcome of competition vary from year to year. GUSTAFSSON termed this effect 'the Montgomery effect', after MONTGOMERY (1912), who noticed this effect at first in his experiments.

3.5. FURTHER ASPECTS OF MIXED CULTIVATION OF BARLEY AND OATS

3.5.1. *The quality of the seed*

The yields of the experiments discussed in section 3.3. are expressed in number of kernels per hectare, because the number of germs determines the reproductive rate in the first place. The change in composition of the mixture in the course of time may differ from the change calculated on basis of the results of a mixed cultivation experiment in one year, if the quality of the seeds which are harvested depends on the composition of the seed mixture.

The germinative power of the harvested seeds was not determined. It appears, however, that the thousand kernel weight of these seeds depends to some extent on the composition of the seed mixture. The relation between the thousand kernel weight of barley and of oats and the value of z_b as determined by averaging the results of the 33 experiments is given in figure 8. The thousand kernel weight of oats appears to increase with increasing values of z_b. Therefore it may be, that oats stand competition somewhat better than calculated.

VAN DOBBEN (1953) explained the effect of the composition of the sown mixture on the thousand kernel weight as follows. Oats growing in a mixture are some time before ripening surrounded by barley plants which are already ripe. These ripe barley plants do not intercept much light and do not use much minerals and water. Oats, which were originally surrounded by a large fraction of barley plants are therefore able to produce during their last weeks of growth more dry matter than oats which are surrounded by oat plants. This can only result in a higher thousand kernel weight because the number of seeds is already fixed at that time.

The effect was very markedly in an experiment on competition between flax *(Linum usitatissimum)* and false flax *(Camelina sativa)* which will be discussed in section 9.1. It appeared that the thousand kernel weight of *Linum* seeds of plants grown in a

mono culture was equal to 6.25 g and of plants grown at a relative seed frequency of 0.27 equal to 8 g and that the thousand kernel weight of *Camelina* was not affected by the relative seed frequency (figure 9).

This difference is explained by the observation that the growth period of *Linum* plants was nearly twice the growth period of *Camelina* plants, so that the *Linum* plants were still growing at the time the *Camelina* plants were ripe.

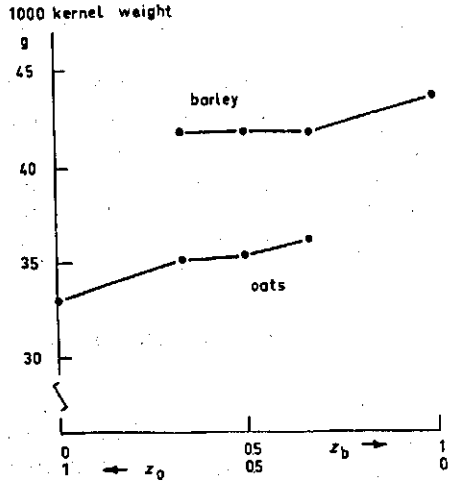


FIG. 8. The thousand kernel weight of barley and oats at different relative seed frequencies. Data from VAN DOBBEN (1951, 1952, 1953 and files).

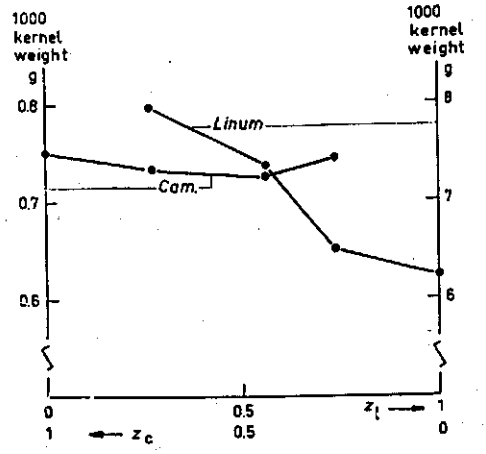


FIG. 9. The thousand kernel weight of flax *(Linum usitatissimum)* and false flax *(Camelina sativa)* at different relative seed frequencies.

As far as the weight of the seeds in the experiments of VAN DOBBEN is concerned, the barley and oat plants do not crowd for exactly the same space. Formally, this means that the sum of A_b and A_o is not constant or one (equation 3.2) but increases somewhat with increasing z_o. It appears here already that to define the term 'space' a time factor is to be introduced.

From a small experiment of MONTGOMERY (1912) who sowed small seeds and large seeds of small grains alone and in competition (his table 13) a value of about 1.2 is estimated for the relative crowding coefficient of the large seeds, with respect to the small seeds, whereas the yields of the mono cultures differed about 8%. The effect of the small difference in thousand kernel weight in the present experiments on the relative crowding coefficient and yields is undoubtedly much smaller and probably negligible.

3.5.2. *The influence of growing conditions on the relative crowding coefficient and the yield of pure stands*

Many other experiments in which barley and oats were grown in monoculture and at a seed ratio 1:1 ($z_b = z_o = 0.5$) were carried out under the direction of VAN DOBBEN (1952, 1953 and 1955).

VAN DOBBEN introduced the *verdringingsfactor* ('crowding coefficient')

$$[O_b O_o^{-1}]\,[M_b M_o^{-1}]^{-1}$$

to characterize the effect of competition at $z_b = z_0 = 0.5$ (present notation). It follows from equation 3.7a that this ratio is an estimate of the *relative* crowding coefficient (k_{bo}) introduced in this paper, if the small systematic difference due to expressing yields in kilograms per hectare, as done by VAN DOBBEN, and in number of seeds per hectare is neglected.

This estimate is, however, not the most efficient estimate because all degrees of freedom are used to estimate k_{bo}, M_b and M_o and not the minimum amount of three. The yields of the pure stands and the value of the relative crowding coefficients are therefore estimated again in the way as described in section 3.3. Only three degrees of freedom are used in this way, so that one degree of freedom (or nearly one because of the correlation between the random error of the yields of barley and oats on the plot with the mixed crop) is left to obtain some impression of the error.

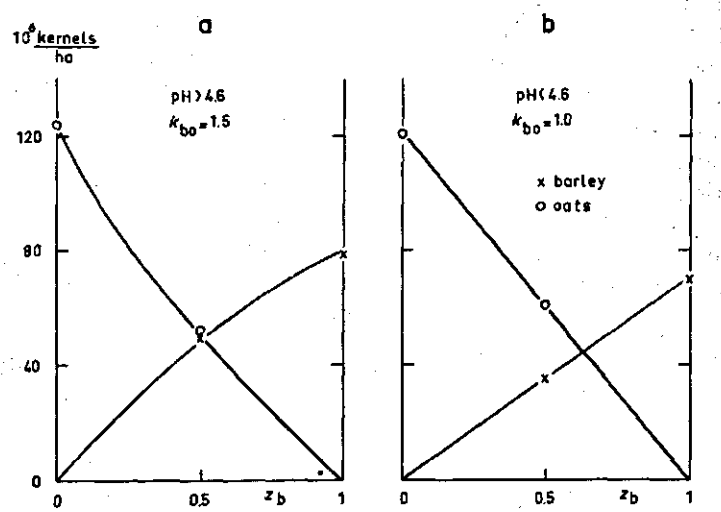


FIG. 10. The average results of the experimental series 163A, 1952 on competition between barley and oats. Data from VAN DOBBEN (1953).
a. pH-KCl larger than 4.6.
b. pH-KCl smaller than 4.6.

The average results of the experiments of series 163A, 1952 (VAN DOBBEN, 1953) are given in figure 10. Figure 10a represents the average results of the experiments with a pH-KCl[1] larger than 4.6 and figure 10b, of those with a pH-KCl smaller than 4.6. Both figures illustrate that in spite of the small number of relative frequencies reasonable estimates of k_{bo}, M_b and M_o can be obtained.

VAN DOBBEN found that the relative crowding coefficient of barley with respect

[1] The pH-KCl is the pH of a mixture of soil and a KCl solution and for sandy soils about one unit lower than the pH of a mixture of soil and water.

to oats (k_{bo}) decreases with decreasing pH of the soil. This effect of the pH is illustrated in figure 10 and may be found in the data given in the caption of figure 7, although it is obscured there by influences of other growing conditions. In order to obtain more information on the influence of the pH, VAN DOBBEN (1955a) carried out an experiment which will be discussed here in some detail.

An experiment, OGe 72, was started in 1931 by the Agricultural Extension Service to study the effect of different nitrogen fertilizers and lime on what is now called the pH of the soil.

The experiment was so successful that the pH-KCl of the soil on the plots varies at present from 3.1 to 5.2. In 1954 VAN DOBBEN divided each plot into three sub-plots, which were sown with either barley (var. Herta), oats (var. Libertas) or a mixture of both in the ratio 1:1 ($z_b = z_o = 0.5$). The value of M_b and M_o, both in number of kernels per hectare and the value of k_{bo} were estimated from the yields on each plot and are given here in the graphs of figure 11, plotted against the pH of the soil.

The yield of the barley appears to decrease rapidly with decreasing pH below a pH-value of about 4 (figure 11a). The yield on the plots which did not receive nitrogen was much lower than on the other plots. As for oats, it appeared (figure 11b) that the yield did not depend to a large extent on the pH and that the yields on the plots which did not receive nitrogen during preceding years was not much lower than on the other plots.

The relation between the pH of the soil and the value of the relative crowding coefficient is given in figure 11c. Throughout the whole pH range, the relative crowding coefficient increases with increasing pH. Above a pH of about 4, the yield of barley nor the yield of oats in mono culture depends to a large extent on the pH. Nevertheless, the relative crowding coefficient increases in the range above a pH of about 4 with increasing pH.

As for the no nitrogen plot with a pH of 4.5 it appears that the value of k_{bo} is equal to one so that the competitive forces of barley and oats matched each other. However, the final yield of barley was about 30% lower than the barley yield on nitrogen plots, whereas this was not the case for oats. Now it is known (VAN DOBBEN, pers. com.; REITH, 1954) that the yield of barley is much more affected by a low nitrogen level during the second half of the growing period than oats. Probably, the nitrogen level on the no nitrogen plots was during the first half of the growing period so high that the barley was able to claim its place, but during the second half so low, that the barley could not realise a sufficient high yield. This suggests that crowding for space takes place during the period of vegetative growth, which is all but unlikely.

The yield of barley grown with oats depends to a much larger extent on the pH than the yield of barley grown in mono culture, because only the yield of barley in the mixture is also adversely affected by the value of the relative crowding coefficient. VAN DOBBEN (1955b) proposed to select barley varieties on their sensitivity for low pH on fields where they are grown in competition with oats in order to increase the effect of the pH. It has not been proved, however, that barley varieties with a high relative crowding coefficient at low pH values or with a relative high yield when grown in competition give also a relative high yield when grown in a pure stand.

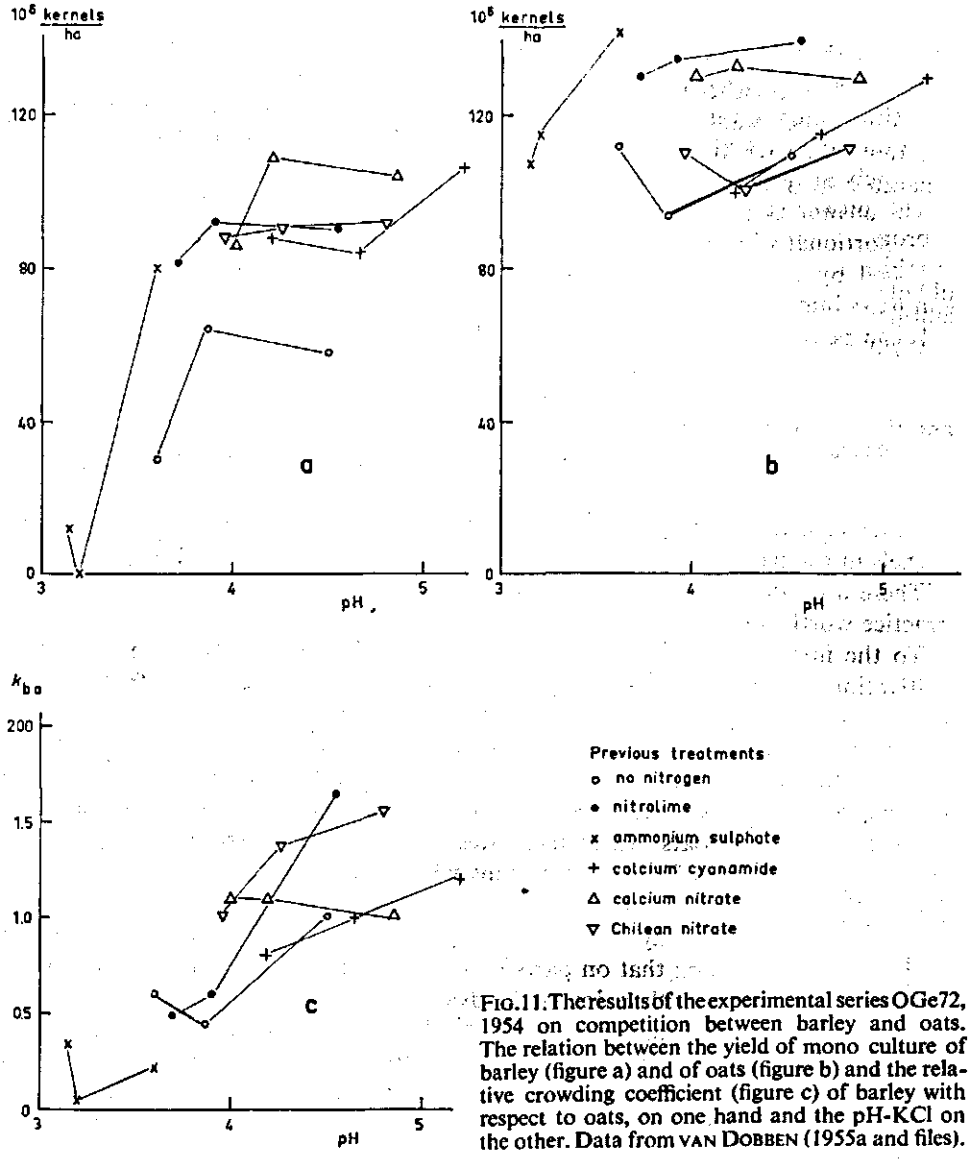


FIG. 11. The results of the experimental series OGe72, 1954 on competition between barley and oats. The relation between the yield of mono culture of barley (figure a) and of oats (figure b) and the relative crowding coefficient (figure c) of barley with respect to oats, on one hand and the pH-KCl on the other. Data from VAN DOBBEN (1955a and files).

3.5.3. *Agricultural advantages*

To evaluate the agricultural value of mixed cultivation of barley and oats, we may suppose for a moment that the thousand kernel weight is not affected by the frequency of the species in the seed.

It follows from formula 3.10 that the total yield ($O_b + O_o$) increases with increasing value of z_b if $M_b - M_o$ is larger than zero and decreases with increasing z_b if $M_b - M_o$

is smaller than zero. The highest yield is therefore obtained, and this holds also for the cash yield, if either the whole field is sown with oats or with barley.

If the farmer wants—for fodder purposes—a mixture of oats and barley, the question arises whether it is more advantageous to grow the barley and the oats separately or in mixed culture.

The answer can be arrived at without mathematics. The yield of barley or oats is proportional with the relative space occupied by these crops. Whether this space is obtained by sowing on separate parts of the fields or by competition in a mixed culture is immaterial.

It can be shown that in both cases the barley yield is equal to

$$O_b = M_b M_o o_b [M_b o_o + M_o o_b]^{-1}$$

and the oats yield is equal to 3.12

$$O_o = M_b M_o o_o [M_b o_o + M_o o_b]^{-1}$$

in which o_b is the fraction of barley kernels in the harvest and o_o the fraction of oat kernels in the harvest.

There are, however, some advantages of mixed cultivation which may make this practice worthwhile.

To the first place it appeared that the thousand kernel weight of oats in mixed cultivation is somewhat higher (figure 8) than in pure stand. Because of this the weight of the oat kernels grown in a mixed culture may be about 36/33 = 1.1 times or about 10% higher than the weight of the oat kernels obtained in a pure stand.

In the second place, it is sometimes difficult to cultivate barley alone, because of lodging and shortness of straw. Lodging is sometimes less if the barley is mixed with a certain portion of oats, which facilitates harvesting considerably and prevent loss of seeds. This is one of the chief reasons why mixed cultivation of barley and oats is practiced in the Netherlands.

In the third place it may be that the pH of the soil of the field differs considerably from place to place and that on parts with a high pH it is advantageous to cultivate barley and on parts with a low pH advantageous to cultivate oats. Under such conditions, it is most simple to sow a mixture of both species so that on spots with a low pH the oats establish themselves and on spots with a higher pH the barley. This seems to be one of the main reasons for mixed cultivation of barley and oats in Denmark (DE WAAL, 1951).

4. CROWDING FOR THE SAME SPACE WITHIN MIXTURES OF HEALTHY AND DISEASED PLANTS

4.0. SUMMARY

It is well known that the yield depression due to the occurrence of a certain percentage diseased plants in a field crop is often lower than the yield depression which would be expected from the depression on fields with 100 percent diseased plants.

It will be shown that this 'compensation power' of the healthy plants can be described quantitatively by means of a relative crowding coefficient of healthy plants with respect to diseased plants. This holds also in the limiting case were the diseased plants do not grow at all.

4.1. SECONDARY LEAF ROLL DISEASE OF POTATOES

REESTMAN (1946) determined the yield of healthy potato plants and the yield of potato plants affected by secondary leaf roll in parts of a field where different fractions of leaf roll diseased plants occurred. It was found by REESTMAN that the yield of a healthy plant surrounded by 50 percent leaf roll plants was higher than the yield of a healthy plant surrounded by healthy plants, and the yield of leaf roll plants surrounded by 50 percent healthy plants lower than the yield of leaf roll plants surrounded by leaf roll plants. The results of the experiments were schematically summarized by REESTMAN in a figure of the same type as our figure 6a.

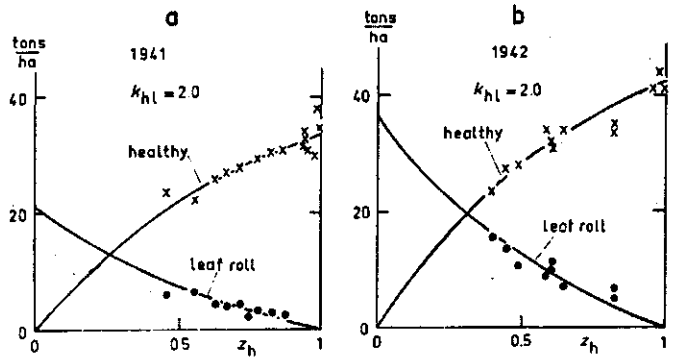


FIG. 12. The relation between the yield of healthy potatoes and potatoes affected with secondary leaf roll as influenced by the relative frequency of healthy plants in 1941 and 1942. Data from REESTMAN (1946).

The results of the experiments with the variety 'Bintje' in 1941 and 1942, recalculated on a hectare basis under the assumption that the number of plants per hectare was 40,000 (REESTMAN, pers. com.) are given in figure 12a and b. The relative frequency of healthy plants (z_h) is given along the horizontal axis and the yield of potatoes in

tons per hectare of healthy plants and plants affected with secondary leaf roll along the vertical axis.

The experimental results may be treated according the competition formulae

$$O_h = k_{hl} z_h [k_{hl} z_h + z_l]^{-1} M_h \text{ and } O_l = z_l [k_{hl} z_h + z_l]^{-1} M_l$$

to obtain an estimate for the relative crowding coefficient of healthy plants in a mixture of healthy plants and leaf roll plants (k_{hl}), the yield of a field with 100% healthy plants (M_h) and the yield of a field with 100% leaf roll plants (M_l). The agreement between the experimental points and the calculated lines shows that the healthy and diseased plants affect each other only by crowding for the same space.

The relative crowding coefficient was in both years 2 and the relative reproductive rate of healthy plants within a mixture of healthy plants and leaf roll plants was (33/21) 2 = 3.1 in 1941 and (42/37) 2 = 2.3 in 1942. As far as the effect of competition goes it should be concluded that the percentage of leaf roll diseased plants decreases rapidly in course of time, which is of course not true because leaf roll is an infectious disease. The relative crowding coefficient (k_{hl}) is larger than one because the adverse affect of growth of secondary leaf roll occurs already at an early stage.

4.2. The effect of leaf rust on the yield of wheat

Klages (1936) cultivated a *Triticum durum* and *Triticum vulgare* variety as mono cultures and in 9 different proportions. The result of the experiment is given in figure 13a, with along the vertical axis the yield in bushels per acre and along the horizontal axis the fraction of *T. durum* (z_d) in the mixtures. The relative crowding coefficient

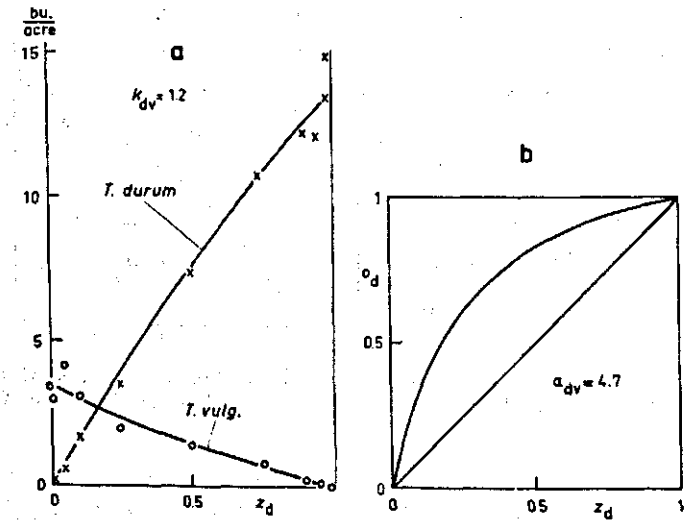


Fig. 13. The relation between the yield of *Triticum durum* and *Triticum vulgare* as influenced by the relative seed frequency of the *durum* species. *Triticum vulgare* was seriously affected by leaf rust. Data from Klages (1936).

of the *durum* variety with respect to the *vulgare* variety appears to be 1.2, so that as far as crowding for space is concerned, the two varieties matched each other. The yield of the *vulgare* variety in mono culture is only 3.6 bushels per acre, compared with a yield of 13.5 bushels per acre of the *durum* variety. This low yield of the *vulgare* variety is, according KLAGES, due to a severe rust attack during the second part of the growing season, the *durum* variety being practically resistent against this rust.

The relative crowding coefficient of about one indicates that during the first part of the growing season the plants of the two species grew equally well, so that at the end of the vegetative period the part of the space occupied by either of the species was proportional with the frequency of each species in the seed mixture. Subsequently, the rust attack affected the growth of the *vulgare* variety to a large extent, resulting in a low yield. At this stage, the plants of the *durum* variety were, however, full grown and not able to take over the space occupied by the *vulgare* variety at an earlier stage. As a consequence, the yield decrease due to the presence of diseased plants was not compensated by a better growth of the healthy plants. This result indicates again that small grains crowd only for space during their vegetative stage of development.

The frequency diagram given in figure 13b, illustrates that the relative reproductive rate of the *durum* variety is very high. It is mentioned here that KLAGES represented his results in such a frequency diagram but did not furnish any theoretical background.

4.3. THE MOST EXTREME FORM OF COMPETITION

Mixtures of two varieties of a plant species, one being susceptible for a certain disease, may be subjected to attacks of different severity. The relative crowding coefficient of the resistent variety will increase with increasing severity of the attack when this disease occurs at a sufficient early stage.

This course of events is already illustrated in section 3.5.2. where the effect of pH and different pre-treatments with nitrogen fertilizers on the competition within barley-oats mixtures was studied. The pH in this case may be understood as 'a soil borne disease which affects mainly the growth of barley'. The results on four sub-plots are given as a further illustration in figure 14. As far as crowding for space goes, the two species match each other under the growing conditions of figure 14a, the relative crowding coefficient of oats with respect to barley (k_{ob} and not k_{bo}) being practically one. This coefficient is already appreciably higher under the conditions of figure 14b. As for figure 14c, the yield of barley is low when grown alone, and negligible when sown with 50 percent oats in the seed mixture; the relative crowding coefficient being increased to three. The most extreme case is reached under the conditions of figure 14d, where barley did not produce a yield either in mixed culture nor in mono culture. The relative crowding coefficient is in this case increased to a value of about twenty.

This relative crowding coefficient is then formally the relative crowding coefficient of oats with respect to barley, but practically the relative crowding coefficient of oats with respect to dead barley or 'empty space not allotted to oats'. In other words:

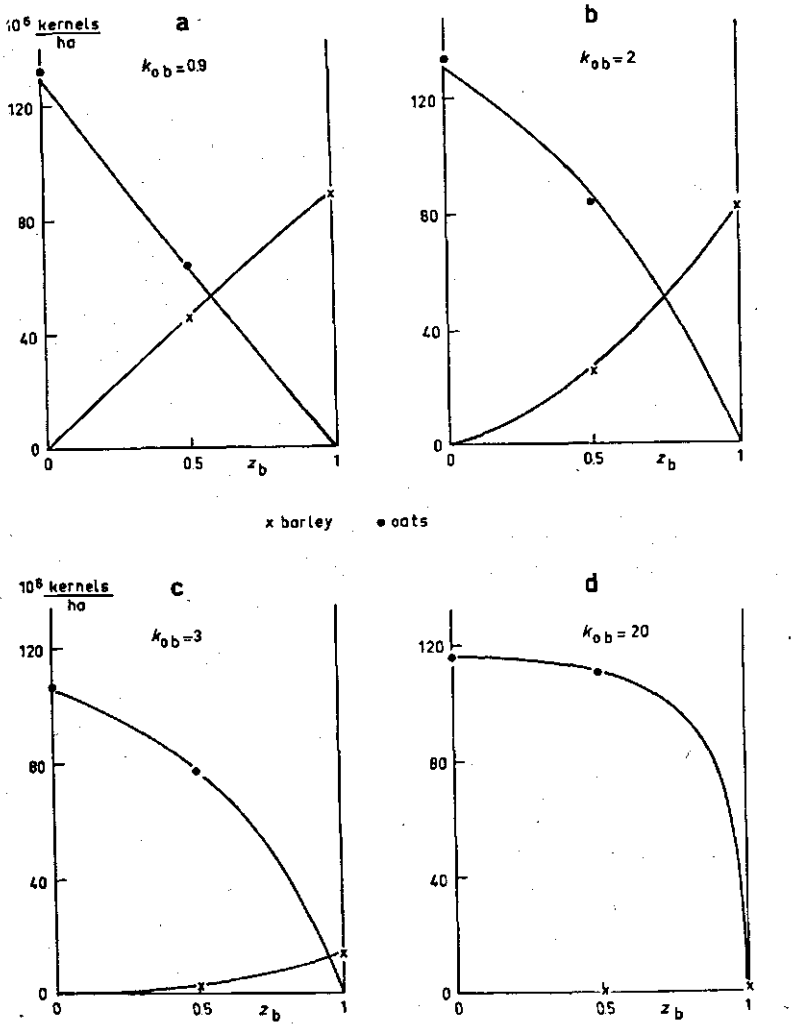


FIG. 14. Competition between oats and barley on four sub-plots of the experiment of figure 11. Data from VAN DOBBEN (1955a and files).
a. Calcium nitrate; pH-KCl = 4.0.
b. Nitrolime; pH-KCl = 3.7.
c. Ammonium sulphate; pH-KCl = 3.2.
d. Ammonium sulphate pH-KCl = 3.1.

the competition experiment between barley and oats is degenerated into a spacing experiment for oats.

Hence there must be a 'degenerated form' of the competition formulae developed in section 3., which is suitable to describe quantitatively the result of spacing experiments.

5. THE INTERPRETATION OF EXPERIMENTS ON SPACING

5.0. SUMMARY

The conclusion of the preceding section, that spacing experiments are a special form of competition experiments is worked out in detail. A formula for the relation between the yield and the seed rate is worked out on basis of some experimental results with small grains.

This formula is applied on the results of some experiments with peas, beets and potatoes to illustrate some important applications and agricultural aspects.

5.1. CROWDING FOR SPACE WITHIN MONO CULTURES

5.1.1. *A spacing experiment with oats*

MONTGOMERY (1912) carried out a spacing experiment with Kherson oats in 1912. The experimental results were:

seed rate	1.25	2.5	5.0	$\times 10^6$ kernels per hectare
yield	47	60	70	$\times 10^6$ kernels per hectare

Seed rates and yields are here given in number of kernels per hectare (supposing that 1 dm^3 oats weights 0.5 kg and that the 1000 kernel weight of oats is 35 g) instead of in bushels and pecks per acre as done by MONTGOMERY. This facilitates comparison with the results of preceding sections.

It may be arbitrary supposed that the unit square of figure 1 (m) equals 20 cm^2 so that for a seed rate of 5×10^6 kernels per hectare each square is planted with one oat kernel; the relative frequency of the squares with oat seeds (z_o) is then equal to one. At a seed rate of 2.5×10^6 kernels per hectare, the relative frequency of the squares with oat seeds is 0.5 and the relative frequency of the 'dead barley seeds' or more correctly of the squares without seeds (z_e, in which the index $_e$ stands for empty square) is also 0.5. Likewise, the relative frequency of the squares with oat seeds is 0.25 and of the squares without seeds 0.75 at a seed rate of 1.25×10^6 kernels per hectare.

According equation 3.4b, the yield of oats may be represented by the formula

$$O_o = k_{oe} z_o \{(k_{oe} - 1) z_o + 1\}^{-1} M_o \qquad 5.1$$

in which M_o is the yield of a field on which all squares of 20 cm^2 are planted with one oat kernel and k_{oe} is the relative crowding coefficient of squares of 20 cm^2 with an oat seed with respect to squares of 20 cm^2 without a seed. The similar equation for the other plant species is of course meaningless, because the squares not planted with oats are not planted at all.

As in section 3.3. it is to be investigated whether there is a value of k_{oe} such that there is a straight line relation between the yield of oats and the space

$$A_o = k_{oe} z_o [k_{oe} z_o + z_e]^{-1}$$

It is seen in figure 15a that this is the case for $k_{oe} = 6$. The relation between the yield of oats and the relative frequency z_o or the seed rate in an auxiliary scale is given in

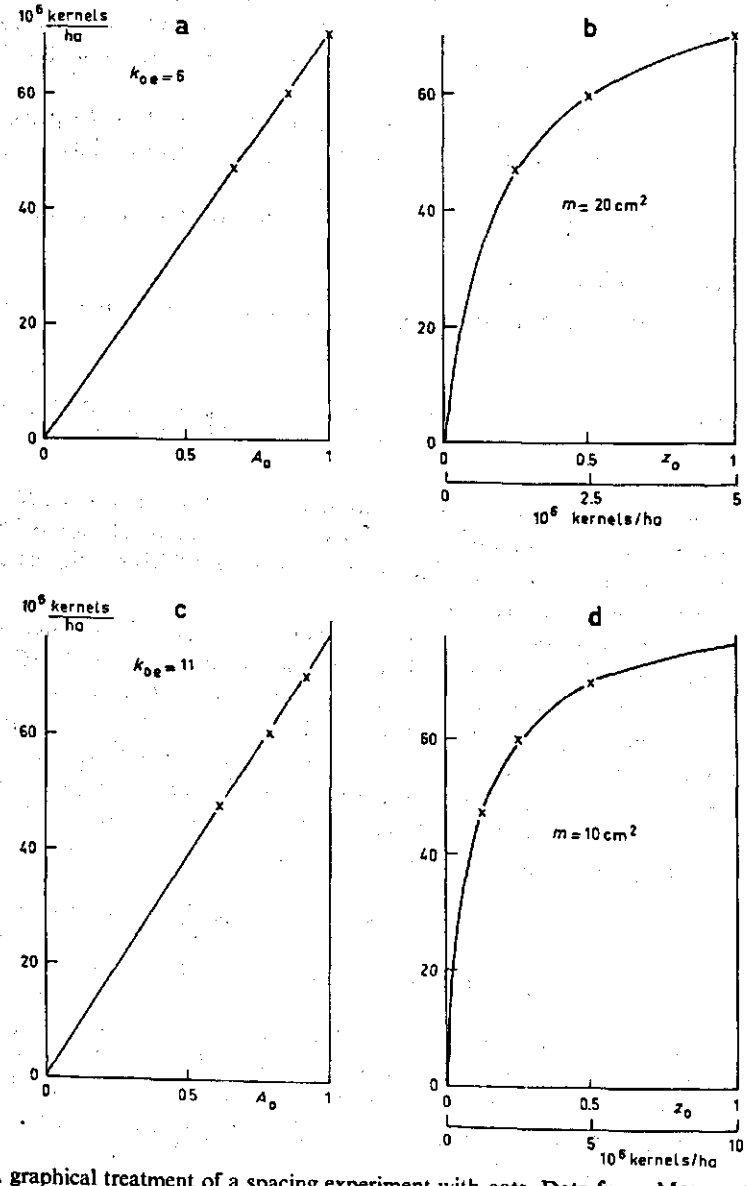


FIG. 15. A graphical treatment of a spacing experiment with oats. Data from MONTGOMERY (1912).

figure 15b. The crosses represent the observational points and the curve satisfies equation 5.1 with $M_o = 71 \times 10^6$ kernels per hectare and $k_{oe} = 6$.

It may be supposed with as much justification that the surface of the unit square is 10 cm² instead of 20 cm² in which case the relative frequencies of the squares with one oat seed are 0.5, 0.25 and 0.125 instead of 1, 0.5 and 0.25. The graphs which are obtained under this supposition are given in figure 15c and d. Now it appears that $M_o = 77 \times 10^6$ kernels per hectare and $k_{oe} = 11$. However, M_o is now the yield of a field on which each square of 10 cm² is planted with an oat seed, and k_{oe} is the relative crowding coefficient of squares of 10 cm² with an oat seed with respect to squares of 10 cm² without seeds. The values of the constants in equation 5.1 appear therefore to depend in a most inconvenient way on the arbitrary choice of the surface (m) of the squares with and without seeds.

5.1.2. *A spacing formula*

Let M_m be the yield per unit surface on a field with a seed on each m cm² and M_s the yield per unit surface on a field with a seed on each s cm² ($s > m$), then $z_o = ms^{-1}$, so that, by substituting these values in equation 5.1, the following relation is obtained:

$$M_s = k_{oe} ms^{-1} \{[k_{oe} - 1]ms^{-1} + 1\}^{-1} M_m = \{[k_{oe} - 1]m + m\}\{[k_{oe} - 1]m + s\}^{-1} M_m$$

Division of the two equations which are obtained by substituting two arbitrary values for s shows that the value of the product $(k_{oe} - 1)m$ is independent of the arbitrary choice of m so that with

$$[k_{oe} - 1]m = \beta \qquad 5.2a$$

the following relation is found:

$$M_s = [\beta + m]\,[\beta + s]^{-1} M_m \qquad 5.3$$

It is now convenient to suppose that the surface of the reference square m is 0 so that

$$M_s = \beta[\beta + s]^{-1} \Omega \qquad 5.4$$

in which Ω is the extrapolated yield at an infinite seed density. The extrapolated reproductive rate of one seed, sown on a very large field is equal to

$$(Ms)_{s \to \infty} = (\beta[\beta + s]^{-1} \Omega s)_{s \to \infty} = \beta\Omega \qquad 5.5$$

The value of Ω is expressed in kernels per cm² or kernels per hectare, but units like kg per hectare, bushels per acre and so on may often do as well. The value of β and the surface per seed is most conveniently expressed in cm² per kernel, but units like ha per kilogram seed or acre per bushel seed, and so on may do also.

According equation 5.4 the following relation holds

$$\beta + s = \beta\Omega M_s^{-1} \qquad 5.6$$

Hence if the inverse of the yield is plotted against the space per seed (or the inverse of the seed rate) a straight line is obtained.

This is shown in figure 16, where for MONTGOMERY's experiment, the space per seed along the horizontal axis is plotted against the inverse of the yield along the vertical axis, both expressed in cm² per kernel. The observational points are found on a straight line. The value of β is now equal to the distance between the origin and the intersection of the line with the horizontal axis and the value of Ω equal to the inverse of the distance between the origin and the intersection with the vertical axis. It appears that $\Omega = 85 \times 10^6$ kernels per hectare and that $\beta = 100$ cm² per kernel.

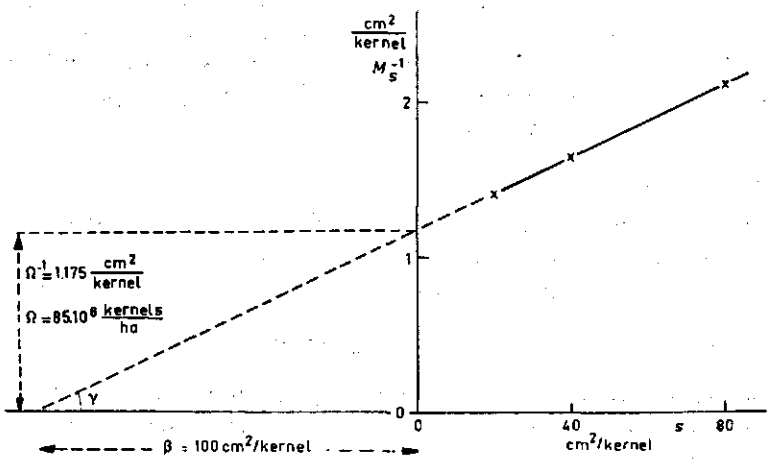


FIG. 16. A graphical treatment of a spacing experiment with oats; the inverse of the yield being plotted against the inverse of the seed rate, that is the space per kernel. The data are the same as those of figure 15.

The reproductive rate of one single kernel should have been 100 cm² kernel^{-1} × 85 × 10⁶ kernels hectare^{-1} = 85. For a unit square (m) equal to 20 cm² a yield of 100 × 120^{-1} × 85 × 10⁶ = 71 × 10⁶ kernels per hectare is calculated, the relative crowding coefficient being according to eq. 5.2a equal to 100 × 20^{-1} + 1 = 6. These values for a unit square (m) equal to 10 cm² are 77 × 10⁶ kernels per hectare and 11, respectively. These values were also found in figure 15.

Because of its simplicity the graphical treatment in figure 16 of the experimental data is preferred, in spite of the distortion of random errors. Where random deviations are relatively considerable (this being always the case at low seed rates), the result is to be checked by plotting data and curve as in figure 15.

5.1.3. *The applicability of the spacing formula*

The relation between yield and space per seed is extrapolated to infinite large and small densities. However, it is well known that at dense seed rates, the yield may decrease considerably with increasing seed rates. This is illustrated in figure 17, where the inverse of the yield in bushels per acre is plotted against the inverse of the seed rate in pecks per acre for an experiment of MONTGOMERY (1912) with Kherson oats in 1907.

Such a yield depression may be due to the existence of some threshold density or space per plant beyond which the plants leave each other such a small space that a normal development is impossible. This is obviously so, where, due to a limited supply of water, narrow spaced plants die during growth but wide spaced plants mature (DE WIT, 1958).

Yield depressions at dense seed rates are, however, in many cases due to density dependent effects of inclement conditions. For instance dense covers are much more

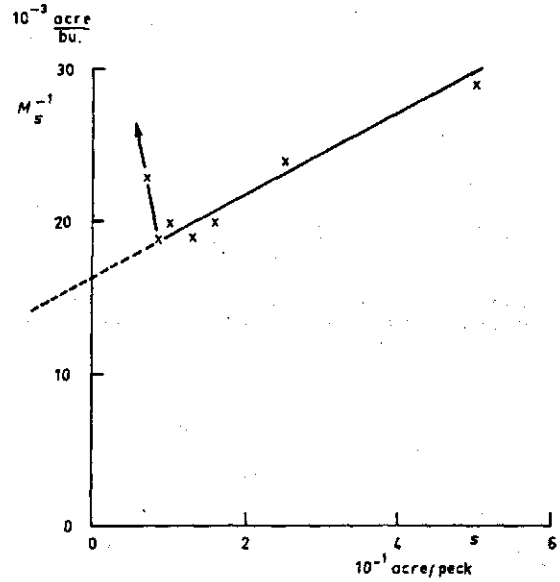


FIG. 17. A spacing experiment with oats, showing a yield depression at narrow spacings. Data from MONTGOMERY (1912).

subject to lodging and subsequent rotting associated with inclement weather conditions than normal covers. This is admirably illustrated by the absence of any depression in the case of some experiments in 1959.

Oats, barley and peas were sown at rates ranging from 1/10 up to 8 times the normal rate, but due to the very fine weather during the whole summer no yield depression occurred, except in one case at the highest seed rate (8 times normal) of oats, as can be seen in figure 18. The relation between yield and seed rate is given here in the normal way, because otherwise the yields at high seed rates can hardly be plotted. The yields are expressed in kg per ha, because the weight of the seeds is more affected by inclement growing conditions during the second half of the growing period than either the number of kernels or the total dry matter weight. Further details on the treatment of these experiments are given in section 8.4.

It is of course also possible that at very low densities yields are affected by density dependent effects of winds, pests and diseases which are not accounted for in the present approach.

There are many spacing experiments with small grains where the distance between the rows is varied, the number of seeds within the rows being the same. It is then

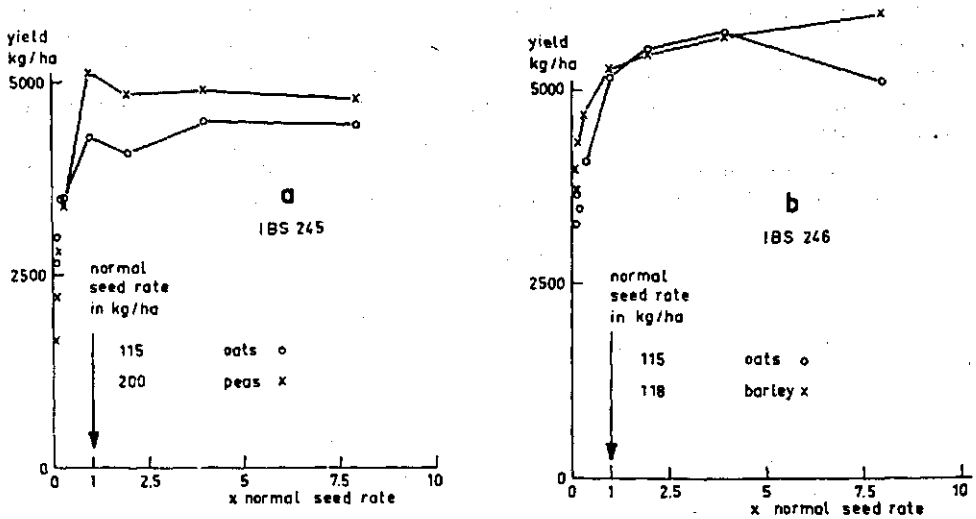


FIG. 18. The result of four spacing experiments with seed rates ranging from 1/10 to 8 times the normal seed rate obtained during the dry summer of 1959. (See also section 8.4.)

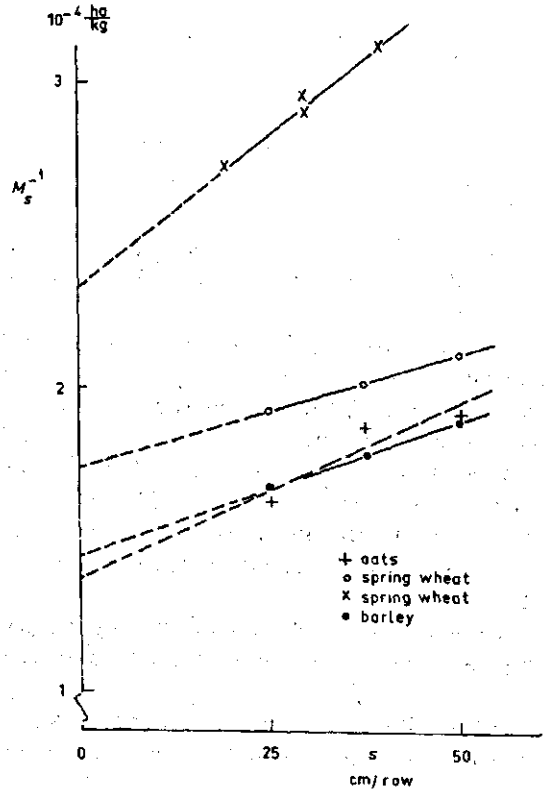


FIG. 19. The result of four spacing experiments with small grains, only the distance between the rows being varied. Data from VAN DOBBEN (1957).

necessary to consider the seed rows, instead of the seed as the 'unit' and to express the inverse of the seed rate in centimeters per row instead of square centimeters per seed. Four such experiments of VAN DOBBEN (1957) with small grains are treated in figure 19. VAN DOBBEN sowed the small grains at a row distance of 25 (or 20) cm and skipped on some plots each third row and on others each second row. The row distances were therefore 25 (20) cm, 25 (20)–50 (40) cm or 37.5 (30) cm on the average, and 50 (40) cm. At one field the row distance was actually 30 cm; the yield difference with the distance 20–40 cm was negligible. The values of β varied here from about 120 cm to even 250 cm per row. This means that the rows are to be sown about 200 cm apart to obtain a yield which is the half of the ceiling yield (Ω).

Hence, to find any effect of spacing on yield, it is necessary to include wide row or seed distances. There are many experiments were the seed rate, row distance or plant number varies only a few ten procent. The results of such experiments are next to useless, because the random errors are large compared with the effect of spacing which can be expected.

5.2. SOME SPACING EXPERIMENTS WITH BEETS

The results of several spacing experiments with beets were discussed in another paper (DE WIT, 1959), so that only the most important aspects will be reviewed here.

PFEIFFER and SIMMERMACHER (1917) reported the fresh weight of sugar beets at widely different plant numbers per surface unit as determined by WOLLNY. The result

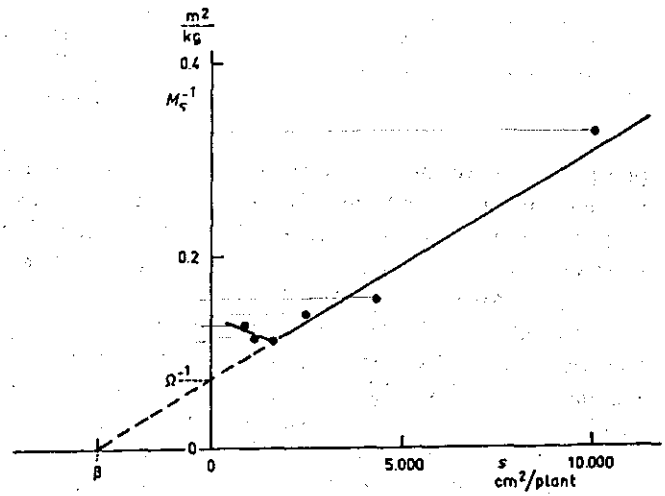


FIG. 20. The result of a spacing experiment with sugar beets. Data from PFEIFFER and SIMMERMACHER (1917).

is given in figure 20 with along the vertical axis the inverse of the fresh weight in m^2 kg^{-1} and along the horizontal axis the space per plant in cm^2 per plant. The yield data for spaces of more than 1600 cm^2 per plant are smoothed by a straight line. At the intersections with the axis it is read that the yield Ω is 140 tons per hectare and the value of β equal to 3000 cm^2. From a space of about 1600 cm^2 per plant (that

is 6.25 × 10^4 plants per hectare) onwards the yield decreases with increasing plant density.

PFEIFFER and SIMMERMACHER (1917) cultivated 1, 3 and 5 beets in containers with a diameter of about 30 cm which were buried in the soil at a distance of 75 cm from each other. The space available for the roots was therefore 700, 235 and 140 cm² per plant and for the leaves 5625, 1875 and 1125 cm² per plant. The observational points in figure 21, where the relation between the inverse of the yield and the space per

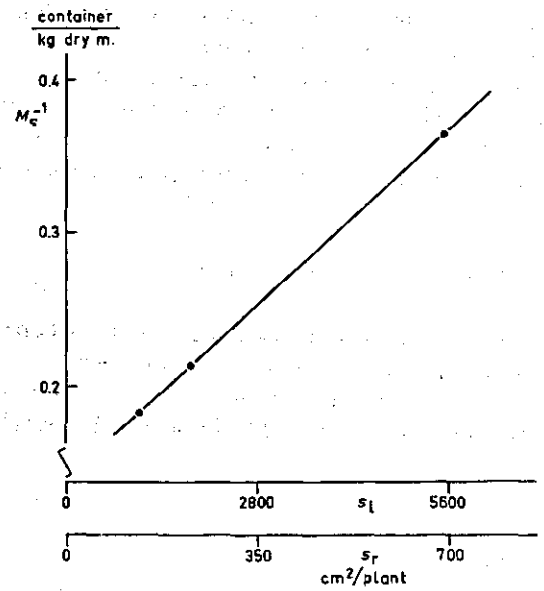


FIG. 21. The result of a spacing experiment with sugar beets.
s_l: space per plant for the leaves.
s_r: space per plant for the roots.
Data from PFEIFFER and SIMMERMACHER (1917).

plant is given are found on a straight line, so that no sign of yield depression due to dense planting can be found. Taking in account the large weight of the beets and the extremely low available space for the roots, it seems that the occurrence of this depression depends on the amount of space available for the leaves and not on the amount of space available for the roots.

The results of a large number of experiments with fodder beets on sandy soils in the south of the Netherlands, published by VAN DILLEWIJN and SMEENK (1944) are summarized in figure 22, with along the vertical axis the inverse of the dry matter yields of the beets in m² kg^{-1} and along the horizontal axis the space per plant in cm². The 21 experiments of 1939 are grouped in experiments with a relatively low, an average and a relatively high yield. The yields for all three levels at the five treatments are represented by full dots. The results of the 10 experiments in 1940 are grouped in experiments with a relatively high and low yield and represented by open dots. The average results of the seven experiments in 1941 are represented by crosses. Throughout the whole traject of spacing and in all three years, the results can be smoothed by straight lines.

The slope of the yield-lines appears to be positively correlated with the inverse of

the yields or negatively correlated with the yield itself. This slope of the line is equal to $(\beta\Omega)^{-1}$ or the inverse of the weight of one plant growing alone (equation 5.5). This correlation between yield level and slope implies that the relative effect of plant density on yields is high when yields at normal plant densities are low.

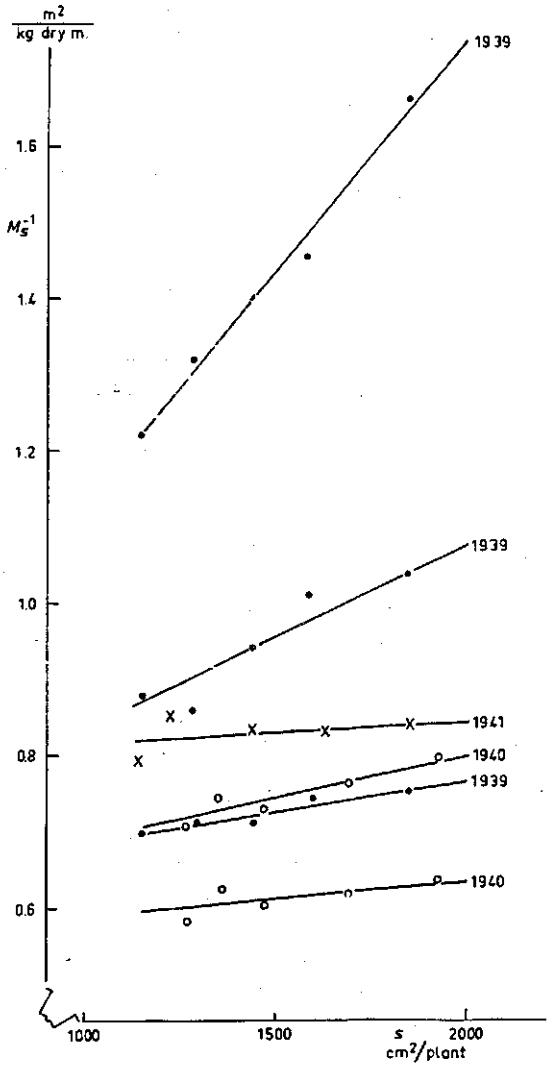


FIG. 22. The average results of spacing experiments with fodder beets on sandy soils in the Netherlands. Data from VAN DILLEWIJN and SMEENK (1944).

This relation between the effect of plant rate and yield level is also found for other plant species, as may be seen in figure 19 and 24. A practical consequence is that, where yield depressions due to dense planting do not occur, it is advantageous to plant or sow at high rates under conditions where yields are low. This is a conclusion which was of course already arrived at by VAN DILLEWIJN and SMEENK (1944).

An interpretation of spacing experiments with sugar beets carried out in the Netherlands appeared to be difficult because yield depressions due to dense planting occurred already at plant rates smaller than 1000 plants per are. A discussion of the results, which are of small importance here, was given in another paper (DE WIT, 1959).

5.2.1. *The value of β throughout the growing season*

It was already remarked in section 3.2. that the relative crowding coefficients characterize not the process of crowding for space itself, but only the result of this crowding.

This is very well illustrated by the change of the value of β during growth, this constant being nothing else than some transformed relative crowding coefficient. At the beginning of growth β is very small, since the seedlings must grow very close together before the growth is affected. At the end of the growing season β is, however, of the order of a few thousand cm^2 per plant. Likewise the value of Ω increases during growth.

The result of spacing experiments which were periodically harvested are to be analysed to obtain some information on the course of the values for β and Ω throughout the season.

VAN GINNEKEN (1934) carried out such an experiment, of which the results are given in figure 23a. The scattering of the observations is relatively large because the plots were small. The observations are smoothed in the following way. A free hand curve is drawn through the observations in figure 23a for each plant density. Subsequently the smoothed yields at the dates 15 July, 1 August, 15 August, 15 September and 15 October are read and plotted in the graph of figure 23b, with along the horizontal axis the space per plant in cm^2 and along the vertical axis the inverse of the yield. These points are smoothed by straight lines and the curves of figure 23a are subsequently corrected. The resulting average curves are given in the figures.

The relations between the date and the values of β and Ω as read in figure 23b are represented in figure 23c, with the date along the horizontal axis and β and Ω along the vertical axis. The scales are chosen such that the observational points at 15 October coincide. It appears that the value of β remains constant from the second half of August onwards, although the weight of the beets (and the value of Ω) still increases. Apparently, the beets are at the middle of August at the end of their development and from that time onwards not capable to occupy more space.

The leaf weight in grams per plant (averaged over the four densities) is represented by open dots in the same figure, such that the maximum leaf weight coincides with the maximum of β and Ω. The points show that the leaf weight remains also constant from the middle of August onwards. This indicates that here β depends on the leaf development.

As for small grains the competition for space takes mainly place during the vegetative period which ends at the beginning of heading. Any adverse effect of diseases, etc. after this stage cannot be compensated for by a better growth of not affected plants. An analogous stage in the development of the beets appears to be the point at which the maximum leaf mass is reached. It must be concluded also that any

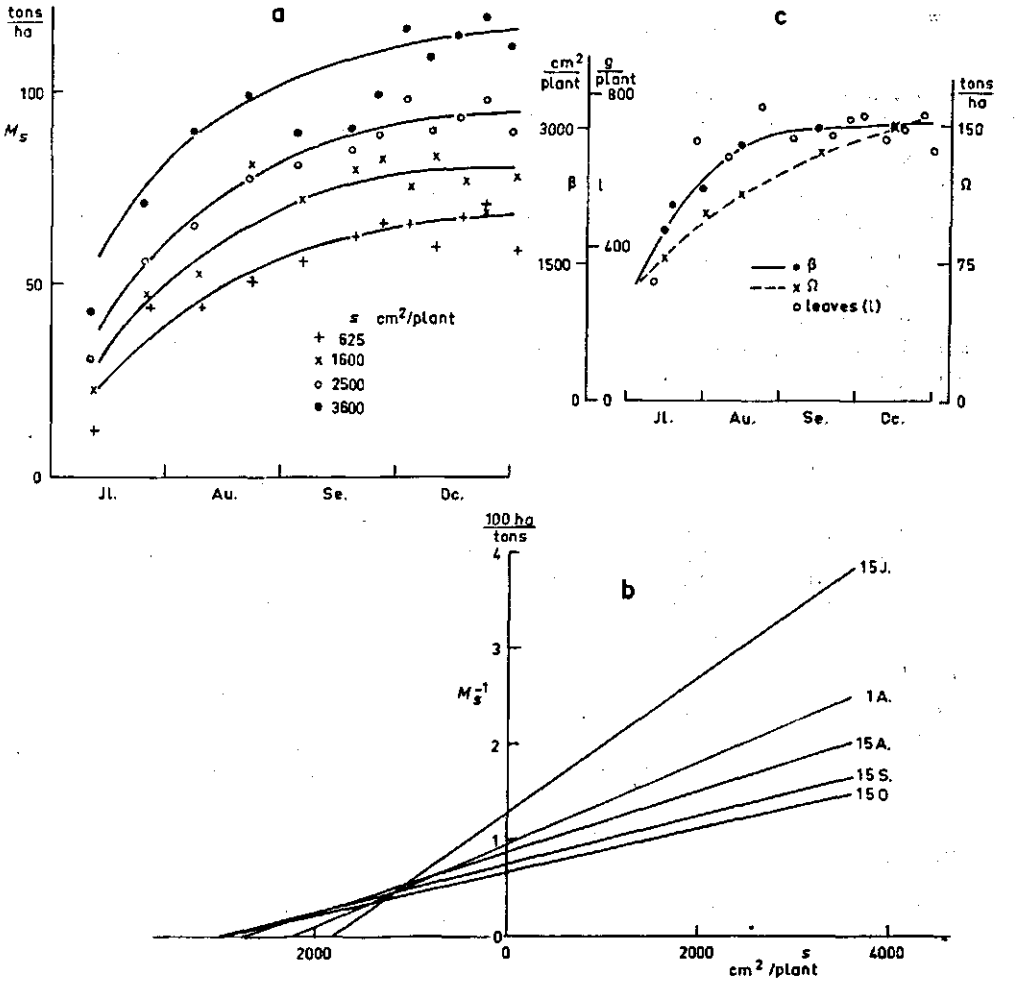


FIG. 23. The result of a spacing experiment with sugar beets harvested at intervals from the beginning of July onwards. Data from VAN GINNEKEN (1934).

adverse effect of diseases, pests, etc. before this time can be compensated to some extent by better growth of not affected plants, but that this is not the case after the leaf mass does not increase any more. It should be taken into account that, although the total leaf mass remains the same, old leaves die and young leaves are growing. It is of course also possible—and in general the rule at the end of the growing season—that the total leaf mass decreases. This is, however, of secondary importance, as far as the present conclusions concern.

5.3. A SPACING EXPERIMENT WITH PEAS

VITTUM *et.al.* (1958) published the result of spacing experiments with peas, carried out in the years 1952, 1953 and 1954. The treatments were:

I. Normal 7 inch row, with a normal seed rate of 3.61 bu per acre.

II. As above, but each second row skipped (14 inch row distance).

III. As above, but each third row skipped ((7 + 14)/2 = 10.5 inch row distance, on the average).

IV. Normal 7 inch row, but with about two third of normal seed rate.

Assuming that 1 hectoliter of the peas weighted 80 kilograms and that the thousand kernel weight of peas was 275 grams, the following surfaces per kernel, and distances between and in the rows are obtained:

Treatment	lbs/acre	kg/ha	cm²/kernel	Distance in cm	
				between rows	in rows
I	3.61	252	109	17.8	6.09
II	1.81	126	218	35.6	6.09
III	2.41	168	164	26.6	6.09
IV	2.54	177	156	17.8	8.75

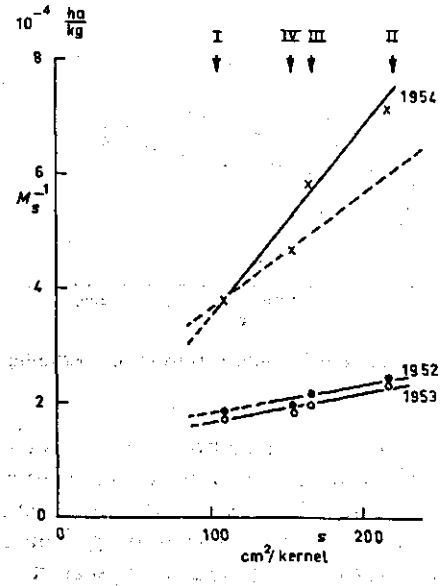


FIG. 24. The result of three spacing experiments with peas. Data from VITTUM *et al.* (1958).

The treatments I, II and III differ only as far as the distance between the rows and the treatments I and IV only as far the distance within the rows is concerned.

The results are represented in figure 24. Along the horizontal axis the surface per kernel in cm² is plotted and along the vertical axis the inverse of the yield in 10^{-4} ha/kg. The observational points for the treatments I, II and III for the three years 1952, 1953

and 1954 are smoothed by the solid straight lines. It appears again that the slope of the line is negatively correlated with the yield level.

The yield of treatment IV with a space of 156 cm^2 per kernel and a distance within the rows of 8.75 cm is in all three years equal to the yield which should have been obtained with a space of about 135 cm^2 per kernel but a distance within the row of 6.09 cm. The deviation from the straight line is the largest for 1954, because in that year the effect of density on yield was relatively the highest.

The solid lines hold therefore only when the row distance is varied, but the distance within the row is kept on 6.09 cm. The broken line, drawn only for the year 1954, holds on the other hand when the row distance is kept on 17.8 cm but the distance within the row is varied.

The cotangent of the angle of the broken line and the horizontal axis is equal to 5.3 gram per kernel. This is the yield of one kernel at a distance between the rows of 17.8 cm, the row being wide apart from any other row. Likewise, it is calculated that the yield of one kernel planted at a distance of 6.09 cm within a row, which is wide apart from other rows, is only 3.1 gram per kernel.

This large difference shows that in spacing experiments it is necessary to plant the seeds either according to a fixed pattern or in rows with the same distance between the kernels, and that an indiscriminate mixture of methods may be very inconvenient.

5.4. Seed rate and yield of potatoes

As for potatoes, the results of several spacing experiments with the variety 'Alpha' carried out from 1956 to 1958, were given by Reestman and de Wit (1959), so that it is not necessary to discuss details in this paper. The relation between plant number and yield depends of the size of the seed piece; the yield from small pieces being much lower than the yield from large pieces especially at low plant densities.

The relation between the inverse of the yield and the inverse of the seed rate, both in are kg^{-1}, is plotted in figure 25a for the average of seven experiments and for the set sizes 25–28 mm (solid dots), 35–45 mm (open dots) and 45–60 mm (crosses). The width of the rows was at all plant densities 60 cm, the planting rate being varied only by varying the distance within the rows.

The value of Ω is 450 are kg^{-1} and appears to be more or less independent of the size of set; which indicates that the yield is independent of the size of the seed pieces at high plant densities. The value of β is, however, 0.37, 0.22 and 0.12 are kg^{-1} for the set sizes 25–28, 35–45 and 45–60 mm, respectively. Large potatoes, planted alone, produce therefore much less per unit weight than small potatoes, so that it must be concluded that the weight of the seed is not a good measure for the seed rate.

It was found (Reestman and de Wit, 1959) that there is a close relation between the yield and the number of stems per unit surface and that the number of stems per seed, when planted alone, is proportional with the surface of skin of the seed pieces. For this reason the seed rate was expressed in surface of skin per unit surface of soil. As a consequence and to account for the size distribution of the tubers produced, the harvest was also expressed in surface of skin per unit surface of soil.

The result is given in figure 25b, which concerns the relation between the inverse of the seed rate and the inverse of the yield both expressed in are of field per m^2 surface of skin. The observations for each size of set are now neatly on straight lines, the deviations being much less than in figure 25a. The value of Ω is again independent of the size of set, and the values of β are 0.93, 0.80 and 0.63 are m^{-2}, for the size of set of 25–28, 35–45 and 45–60 mm, respectively.

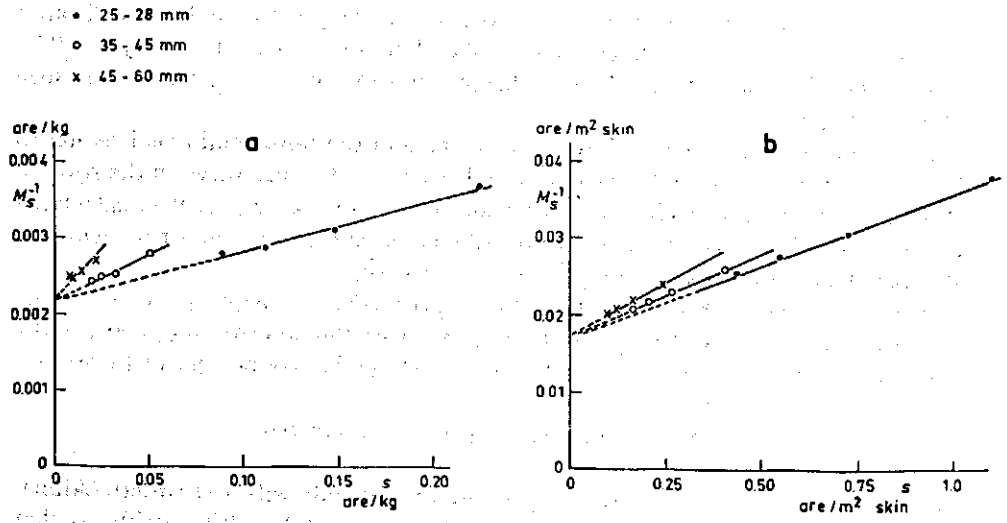


FIG. 25. The average result of spacing experiments with potatoes (1 are = 10^{-2} hectare).
a. Based on weight of the tubers.
b. Based on surface of skin of the tubers.
Data from REESTMAN and DE WIT (1959).

Especially the value of β for the largest sets is smaller than for the smaller sets. The potato stems are distributed in groups of five to ten in case of large sets, whereas with small seed pieces the stems are distributed in groups of one to two. Apparently, the large reserve per unit surface of skin for large seeds, cannot be used to overcome completely the disadvantage of irregular distribution of the stems.

The yield of large seed pieces may be improved by better distribution of the stems obtained by cutting. When the pieces are cut to the weight of seeds of small sets, the yield is lower than for small sets planted at the same number. On the other hand, if large sets are cut such that the surface of skin of the pieces is equal to the surface of skin of small sets, the yield is the same as the yield from small sets planted at the same number (REESTMAN and DE WIT (1959)).

6. THE GROWTH OF POPULATIONS

6.0. SUMMARY

The time-yield relation which is obtained by resowing again and again the harvest, starting from one plant, is studied. It will be shown that this relation is the same as the PEARL-VERHULST equation of logistic population growth. Some classical experiments on the growth of yeast and *Drosophila* populations will be interpreted as spacing experiments.

The applicability of the logistic equation in animal population dynamics is compared with the applicability in agriculture.

6.1. A TIME SERIES

Let it be supposed that in the spacing formula

$$M_s = \beta[\beta + s]^{-1}\Omega \qquad 5.4$$

the value of Ω is 100 kernels per unit surface and the value of β is 0.02 unit surface per kernel.

Provided that growing conditions are the same during a number of years and that stochastic effects are absent, the number of kernels $[M_{t+1}]$ which is obtained in the $[t+1]$th year by resowing the harvest $[M_t]$ of the t th year may be calculated by means of the formula

$$M_{t+1} = \beta[\beta + M_t^{-1}]^{-1}\Omega \qquad 6.1$$

which is the same as formula (5.4) but for M_s and s being substituted M_{t+1} and M_t^{-1}.

The result is represented in figure 26 with along the vertical axis the number of kernels per unit surface and along the horizontal axis the number of years, supposing the first year being started with one kernel.

The number of kernels appear to approach a maximum, which is equal to $[\Omega - \beta^{-1}]$. Any disturbancies around the maximum due to adverse effects of dense seed rates are not taken into account. It is a matter of course that in actual experiments such disturbancies play a dominant part and that yields do not approach to this maximum but may show a more or less cyclic variation around this maximum. The shape of the curve is very similar to the well known sigmoid curves of population growth, a similarity which is studied in detail in the next sections.

6.2. TWO CLASSICAL EXPERIMENTS ON POPULATION GROWTH INTERPRETED AS SPACING EXPERIMENTS

PEARL (1930) was able to carry out experiments on population growth of *Drosophila* in pint bottles nearly through to completion by adding food skilfully and in small

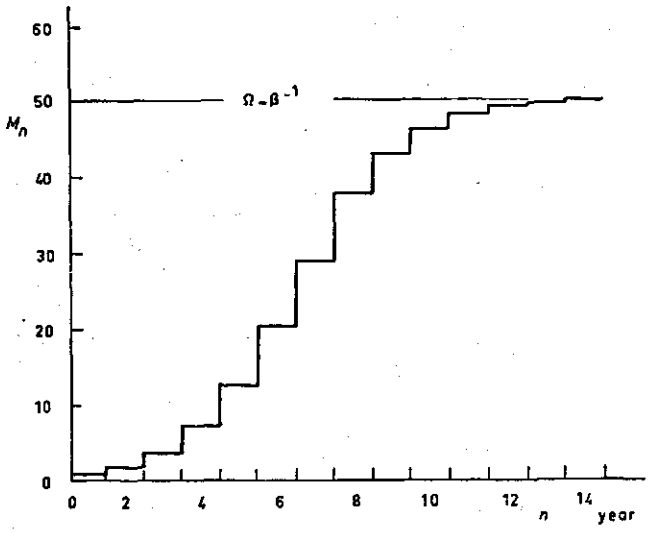


FIG. 26. The relation between yield and time in years which is obtained by resowing the harvest of the previous year.

The curve is calculated by substituting in the spacing formula a value of 100 kernels per unit surface for Ω and of 0.02 unit surface per kernel for β.

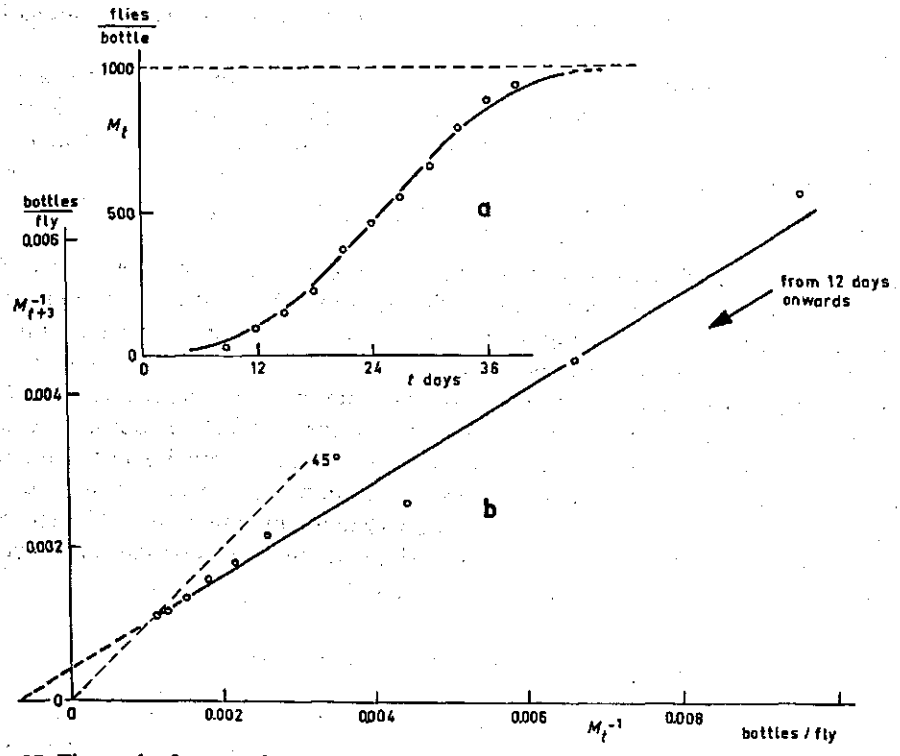


FIG. 27. The result of an experiment on the growth of a *Drosophila* population, plotted as a growth curve (figure a) and treated as a spacing experiment (figure b). Data from PEARL (1930).

amounts. The result of one of his experiments (PEARL's table 10) is represented in figure 27a. The number of flies per bottle, as determined by counting, is given along the vertical axis, and the number of days since the introduction of a small population along the horizontal axis. The observations were done with three days intervals except on two occasions around Christmas and New Year. For reasons which are obvious later on, it is necessary to work with equal intervals between sample dates, so that a number of 499 flies on the 25th day, is here replaced by a number of 465 flies on the 24th day and a number of 618 flies on the 29th day by 650 on the 30th day.

Disregarding for biological (PEARL, 1930) and statistical reasons (section 6.4.) the data for the first sampling dates, it may be supposed that PEARL executed a spacing experiment, in which the harvest (being here all the living material) at the ninth day was resown directly afterwards, the bottle again harvested at the twelfth day, the harvest resown again, and so on the 15th, 18th to the 39th day.

If a *Drosophila* population reacts in the same way on spacing as plants do, so a straight line would be obtained if the inverse of the yield on the 9th day, is plotted against the inverse of the yield on the 12th day, the inverse of the yield on the 12th day against the inverse on the 15th day, and so on, taking care of course to compare only samples with the same time interval in between.

This is done in figure 27b from the 12th day onwards. The observations are actually close to the straight line which is drawn through the points. The *Drosophila* experiment may be interpreted therefore as a simple spacing experiment, or in other words: the intraspecific competition within the *Drosophila* population of the pint bottle may be interpreted as an interspecific competition between the *Drosophila* population and 'empty space, (see section 4.3.). Citing NICHOLSON (1954), 'growth is here governed by space or by a transient requisite which gives a constant favourable quality to space, like food added in small amounts'.

The values of Ω and β as read at the intersections with the vertical and horizontal axis are 2500 flies per bottle and 0.00067 bottles per fly. The number of flies can never be larger than the number which is indicated by the intersection of the line with the 45 degrees line dotted in figure 27, because at this point the number of flies harvested is the same as the number of flies sown. This maximum number of flies is read to be 1000 flies per bottle and in the following represented by the symbol K. Of course, the straight line relation may be disturbed before this density in actual experiments, because of overcrowding or deterioration of the environment. This is actually the reason why PEARL finished his experiments before the maximum value was reached.

The tangent of the yield line with the horizontal axis is equal to $(\beta\Omega)^{-1}$ so that

$$K^{-1} = [\beta\Omega]^{-1}[\beta + K^{-1}] \text{ or } K = \Omega - \beta^{-1} \qquad 6.2$$

For the present example this maximum appeared to be indeed $2500 - (0.00067)^{-1} =$ 1000 flies per bottle.

The smoothed relation between the number of flies and the number of days may be found as follows. On the t-th day the number of flies may supposed to be 167, so that the inverse is equal to 0.0060. It is then read in graph b that the inverse of the number of flies on the $(t + 3)$th day is 0.0041 or the number itself 244 flies per bottle.

Likewise it is read that on the $(t - 3)$th day the inverse of the yield is 0.0091 and the yield itself 110 flies per bottle. The yield on the $(t + 6)$th and $(t - 6)$th day and so on may be read now in the same way. The relation between the number of flies per bottle and the time may now be drawn on transparent paper with the same scale as figure 27a. To adjust the time scale or to eliminate the arbitrary time t, the transparent graph is shifted horizontally over the graph with the observations (figure 27a) until a good fit is obtained. The curve obtained in this way is drawn in figure 27a, where it is seen that the resulting curve fits the observations quite well.

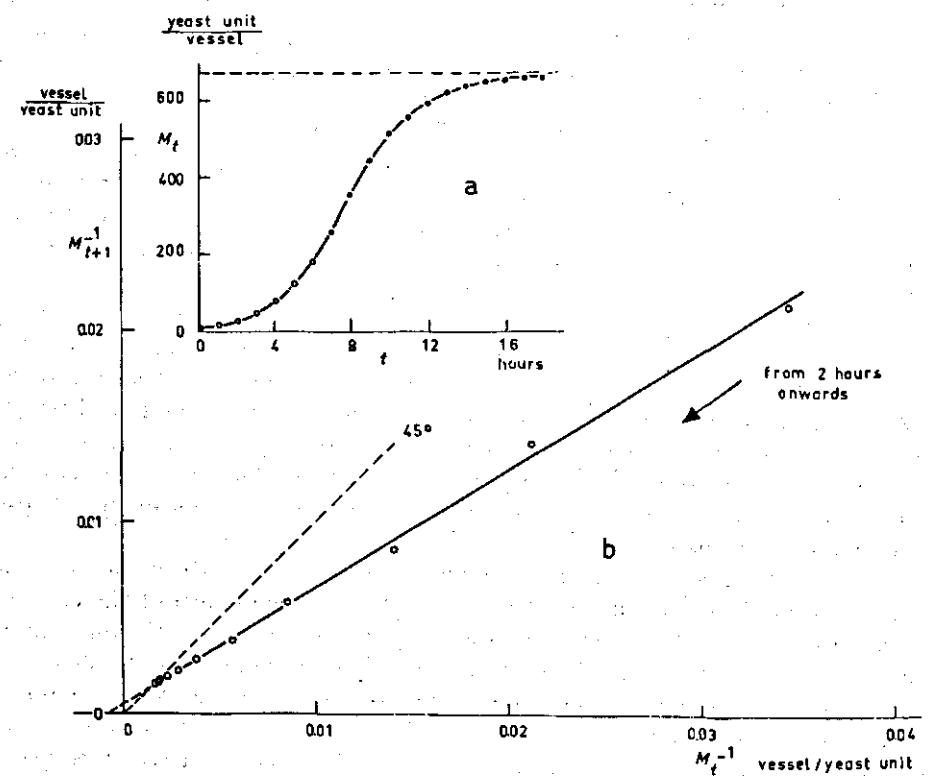


FIG. 28. The result of an experiment on the growth of a yeast population, plotted as a growth curve (figure a) and treated as a spacing experiment (figure b). From data cited by PEARL (1930).

PEARL reports in his table 4 also the results of an experiment with yeast.

These results are represented here in figure 28a. In figure 28b the inverse of the yield at the second hour is plotted against the inverse of the yield at the third hour, the inverse at the third hour against the inverse at the fourth hour and so on. The observations are again on a straight line. At the intersection with the dotted 45 degrees line it is read that the maximum yeast population (K) was 660 yeast units per vessel and from the slope of the line it is read that $(\beta\Omega)^{-1}$ is equal to 0.635, so that with equation 6.2 it is calculated that β is equal to 0.00087 vessels per yeast unit and Ω equal to 1800

yeast units per vessel. These values may be read also at the intersections with the horizontal and vertical axis, but with less accuracy. The relation between population growth and time is reconstructed in the same way as is done for the *Drosophila* population and given in the graph of figure 28a. The growth of yeast is inhibited by its alcohol production, so that at its maximum density the yeast is in a state of rest, which explains why here any random or cyclic scattering around the maximum is absent.

6.3. The logistic curve

Sigmoid curves of the above type are in general described on basis of the logistic differential equation (Lotka, 1925; Volterra, 1928; Pearl, 1930; and many others):

$$dM_t(dt)^{-1} = rM_t[K - M_t]K^{-1} \qquad 6.3$$

in which r is the coefficient of increase which a population would have if ample space, that is 'food' (see section 3.2.) is available, K the maximum or equilibrium density under the conditions of growth and M_t the yield on time t.

A solution of this equation is the following

$$M_{t+\Delta t}[M_{t+\Delta t} - K]^{-1} = M_t[M_t - K]^{-1}e^{r\Delta t} \qquad 6.4$$

in which $M_{t+\Delta t}$ and M_t are yields at two moments, of which the time interval is represented by the symbol Δt. This equation may, with $M_{t+\Delta t}$ explicite, be rewritten as follows:

$$\begin{aligned} M_{t+\Delta t} &= Ke^{r\Delta t}\, M_t\{K + [e^{r\Delta t} - 1]M_t\}^{-1} = \\ &= [e^{r\Delta t} - 1]K^{-1}\{[e^{r\Delta t} - 1]K^{-1} + M_t^{-1}\}^{-1}Ke^{r\Delta t}[e^{r\Delta t} - 1]^{-1} \end{aligned} \qquad 6.5$$

so that by substituting:

$$\begin{aligned} \beta &= [e^{r\Delta t} - 1]K^{-1} \\ \Omega &= Ke^{r\Delta t}[e^{r\Delta t} - 1]^{-1} \end{aligned} \qquad 6.6$$

the following relation is obtained

$$M_{t+\Delta t} = \beta[\beta + M_t^{-1}]^{-1}\Omega \qquad 6.7$$

This relation is identical with our equations 5.4 and 6.1.

Consequently, logistic growth of animal populations can only occur if the growth is only and promptly governed by the space (or some transient requisite associated with space) the animals secure by means of 'scrambling' (compare Nicholson, 1954).

The value of $(\Omega - \beta^{-1})$ is indeed equal to K, whereas

$$\beta\Omega = e^{r\Delta t} \qquad 6.8$$

$\beta\Omega$ was also equal to cotg γ (figure 16) so that the slope of the lines in figure 27 and 28 and the values of the constants β and Ω appear to depend on the length of the time interval chosen, a conclusion which in its qualitative form is obvious.

6.4. THE APPLICABILITY OF THE LOGISTIC MODEL

There are many experiments on growth of animal populations which cannot be described by means of the logistic model (compare for instance ANDREWARTHA and BIRCH, 1954; NICHOLSON, 1954). It is therefore not surprising that animal ecologists, convinced as they are from the complexity of their subject, are sceptical as to the applicability of the logistic theory or sometimes even to the usefulness of any theories. On the other hand, it was found in this paper that the spacing formula, being a special solution of the logistic differential equation is, as far as the effect of density on the growth of plants is concerned, of wide applicability, in spite of the fact that the growth of plants is in itself not less complicated than the growth of animals. The reason of this difference in usefulness of the logistic theory is due to the different experimental approach.

In spacing experiments, seeds are sown in one season at different densities and this seed rate is only related with the yield of similar seeds at maturity. So, the experiment is completed with one generation and the data concern only those parts of the plant, which stay over during some dormant or winter season. In experiments on population growth, however, a medium provided with a constant rate of a transient requisite is inoculated with a small amount of the species concerned which are left to develop, census counts being taken at intervals.

It is evident, that during such growth experiments, the condition of the medium must be kept the same, although the presence of the population results in irreversible changes of the medium. To keep the medium the same, it is necessary to change this medium frequently. In general, techniques are developed where the changing of the medium and the addition of the transient requisite (in general food) is combined. If one succeeds sofar with the experiment it may be (as found by FRANK (1957) with experiments with *Daphnia*) that the properties of the population depend on the period it is living in the medium. As for spacing experiments, there is no such change of the medium and no adaptation of the species with respect to the growing conditions, because the experiment is completed in one season with one generation.

In a medium of an experiment on growth of for instance insects populations there are eggs, larvae, puppae, and adults which proportions may or may not change during growth. Under such conditions, it is often difficult to obtain census counts, because it is often impossible to know whether biomass, number of adults, number of individuals and so on are to be weighted, measured, counted and so on. A plant passes also many stages of development from germination until ripening. However, to study the effect of spacing on the multiplication of the plant species, it is only necessary to consider the seed rate and the harvest rate. It is admitted that sometimes, as is the case with small grains, the rates are to be expressed in number of seeds per surface unit of the field, or, sometimes, as is the case with potatoes, in surface of skin per surface unit of the field, and that with other plants other ways of measure may be the most useful. However, it is only necessary to consider the parts of the plants which stay over during the winter or dormant season. It is not necessary to study the growth phenomena itself, in order to develop the general laws considered in this treatment.

Spacing experiments can be carried out with animals. One may take animals in the form as they stay over their 'dormant' or 'winter' season, 'sow' these animals at different rates in a suitable medium and determine the 'yield' of offspring after one or may be a few generations. It depends of course on the species, whether this 'yield' of offspring is to be expressed in number of individuals, weight of the individuals, fertility of the individuals or such a measure. The data collected in this way may be treated as the data of a spacing experiment with field crops. If, which is of course not necessarily so, the relation between inverse of the 'seed rate' and the inverse of the 'yield rate' is a straight line it is possible to calculate the values of β and of Ω and from these the parameters of the normal logistic equation, which are the saturation rate (K) and the initial rate of increase (r).

Since under the conditions of such experiments, 'space' (or a transient requisite associated with space) will be in general the main governing factor, it is to be expected —as is the case with plants—that in many cases logistic relations result.

This logistic relation must be interpreted in its own rights, taking in account the conditions of the experiment. It must be realised that such an experiment gives no information at all on 'conditioning' either of the medium nor of the animal species.

Of course there are still experimental difficulties. In the first place there may be unavoidable pests, diseases and so on, of which the effects may be density dependent. As far as field experiments with plants are concerned, the occurrence of those is all but unlikely. In the second place there may be, especially in case of animals, a treshold density beyond which the growth is abnormal, because too small an amount of a necessary requisite is available for each individual. The resulting effects must be treated along the same lines as oscillatory scattering around the saturation rate in experiments on growth, and need no further consideration here.

At last it must be mentioned that the growth of small experimental populations may to a large extent be affected by random factors. These effects have been studied recently by BARTLETT (1957), LESLIE (1958) and LESLIE and GOWER (1958) which are mentioned here because their statistical views run to some extent parallel with the present approach.

These investigators also derived from the logistic differential equation, equation 6.7 and they supposed that the growth during the time interval Δt is not only determined by this equation but also by some stochastic or random term. Some models for this stochastic term have been developed, and in step by step calculations the census counts ('yields'), as affected by this stochastic term, were substituted. By such 'Monte Carlo' processes, a random logistic may be obtained, of which the behaviour can be studied and compared with actual experimental growth curves. LESLIE (1958) came to the conclusion that the mean values of a random logistic can be fitted by any ordinary logistic curve, and that the estimates of the parameters for these experimental logistics gradually approach the true values of the process as numbers increase in magnitude. For a large population we might conclude according to LESLIE that to a fairly close approximation the deterministic model is for all practical purposes the same as the mean stochastic model. These conclusions hold, of course also for spacing experiments as considered here.

6.5. Another approach

A team of the Institute of Polytechnics of the Osaka University in Japan, working on intraspecific competition among higher plants described the results of their spacing experiments with the so-called density-effect law which is represented by one of the following two equations:

$$w\rho^a = C \text{ or } y\rho^{a-1} = C \qquad 6.9$$

in which w, y and ρ denote the average plant weight, total plant yield per area and the density of plants (i.e. number of plants per area), respectively[1]. Both a and C are constants depending on duration of growth after seeding, the former being called the competition-density (C-D) index. With the progress of time, the value of the C-D index should increase from 0 at $t = 0$ to about 1 at $t = \infty$. For $a = 1$ the second equation degenerates into the equation

$$y = C$$

which lead to the conclusion that ultimately the yield of a field is independent of the density of planting. This may be of course for a field of grassland, giving sufficient time to develop but it seems to be an over-simplication for crops which grow only one season.

Shinozaki and Kira (1956) developed on this basis a logistic theory of the C-D effect.

They assumed in the first place that the growth of a plant in dry weight (w) is represented by a simple logistic equation, viz.

$$dw(dt)^{-1} = \lambda w[W - w]W^{-1} \qquad 6.10a$$

with the solution

$$w = W[1 + ke^{-\lambda t}]^{-1} \qquad 6.10b$$

where W is the asymptote and λ is the initial rate of increase. Both W and λ are constantly independent of time. The integration constant k is determined by the initial condition. In the second place it is assumed that the coefficient of growth of a single plant is independent of the density of planting (ρ), and in the third place that the ultimate yield per area ($(y)_{t\to\infty} = Y$) is constant, that is

$$\rho W = Y \text{ is independent of } \rho \qquad 6.11$$

At last it is of course assumed that the weight of each seed, sown at the time $t = 0$ is independent of ρ, that is

$$(w)_{t=0} = w_0 \text{ is independent of } \rho$$

[1] The symbols of the original paper are maintained, to avoid confusion.

From these rather arbitrary assumptions an equation describing the relation between plant density and weight is arrived at in the following way:

Let $t = 0$ in equation 6.10b then

$$w_0 = W[1 + k]^{-1} = Y\rho^{-1}[1 + k]^{-1}$$

so that

$$k = Y[w_0\rho]^{-1} - 1 \qquad 6.12$$

By substituting equation 6.11 and 6.12 in equation 6.10b the following relation is obtained

$$w^{-1} = Y^{-1}[1 - e^{-\lambda t}]\rho + w_0^{-1}e^{-\lambda t} \qquad 6.13$$

Putting in equation 6.13

$$A = Y^{-1}[1 - e^{-\lambda t}] \qquad 6.13.1$$

$$B = w_0^{-1}\, e^{-\lambda t} \qquad 6.13.2$$

the relation

$$w^{-1} = A\rho + B \qquad 6.14$$

is found between the weight per plant (w) and the density (ρ), so that the yield per area is given by the following equation:

$$y = \rho[A\rho + B]^{-1} \qquad 6.15$$

By putting

$$s = \rho^{-1} \quad \Omega = A^{-1} \quad \beta = AB^{-1} \text{ and } M_s = y$$

the spacing formula

$$M_s = \beta[\beta + s]^{-1}\Omega \qquad 5.4$$

arrived at in section 5.1.2. is obtained.

The ultimate yield Y, reached at $t = \infty$, assumed to be independent of density of planting, is according the equation 6.13.1 ($t = \infty$) equal to A^{-1} or nothing else but our yield ceiling Ω. The constant B is equal to $(\beta\Omega)^{-1}$ or the inverse of the weight of a single plant, growing alone.

According to eq. 6.13.2 of SHINOZAKI and KIRA this weight of a single plant should increase exponentially with time, beyond all limits. This is evidently impossible, but not at variance with their eq. 6.10b, because it is assumed (see eq. 6.12) that the constant k increases beyond all limits with decreasing density. It is proved, however, that in stead of eq. 6.11 the relation $[\rho + \delta]W = Y$, in which δ is a constant, suffices to arrive at eq. 6.15.

The authors test their spacing formula by plotting the inverse of the yield per plant against density, as done in figure 29. The observations arrange indeed around a straight line which furnishes a proof of the usefulness of their formula 6.14 and 6.15 and of course also of the spacing formula 5.4 arrived at in the present paper.

The authors suggest that in this way the correctness and necessity of their initial set of assumptions is proved. However, the same spacing formula is arrived at in section

5.1.2. and tied up with the logistic equation in section 6.3 without making any assumptions regarding the seasonal growth of the plants. Whether this growth is logistic or not is completely immaterial.

Apparently, the applicability of an equation as this spacing formula does not prove the correctness of a set of underlying assumptions. On the contrary, care should be

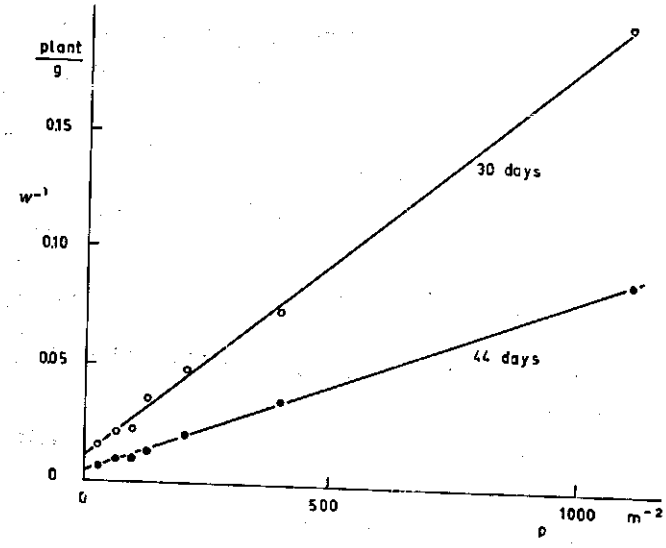


FIG. 29. The result of a spacing experiment with carrots, the inverse of the yield per plant (w^{-1}) being plotted against the plant density (ρ). (Redrawn after figure 13 of SHINOZAKI and KIRA (1956).)

taken to confront each step of a descriptive approach with practical experience, and to avoid in first instance any explanation of the relations.

BLEASDALE and NELDER (1960) found that the relation $w^{-\theta} = A\rho^{\theta} + B$, where θ is some positive quantity usually less than unity, frequently gives a strikingly better fit than eq. 6.14 to the data from spacing experiments. This relation can be arrived at from a generalization of the logistic equation, described by RICHARDS. The authors work along the same lines as SHINOZAKI and KIRA. Details are not given, but it is likely that here also the approach of section 6.3. may do better.

The data in this paper do not cover a sufficiently wide density range to judge the advantage of this modification, nor is it possible to do this for an extension of this modification to competition problems.

7. CROWDING FOR THE SAME SPACE WITHIN MIXTURES OF MORE THAN TWO SPECIES

7.0. SUMMARY

The equations describing the effect of crowding for space within mixtures of two species may be extended to mixtures of more than two species. The experimental data which are given do not prove the applicability of the model, but illustrate only its qualitative aspects.

7.1. THE BASIC EQUATIONS

In analogy with the equations for multicomponent mixtures (section 2.2.) and the equations 3.2 (section 3.2.) for crowding for space within a mixture of two species, the following equations may be written if n species affect each other only by crowding for the same space.

$$A_1 : A_2 : \ldots : A_k : \ldots : A_n = b_1 Z_1 : b_2 Z_2 : \ldots : b_k Z_k : \ldots : b_n Z_n \qquad 7.1a$$

$$\sum_{k=1}^{n} A_k = \text{a constant} = 1 \qquad 7.1b$$

$$\sum_{k=1}^{n} Z_k = m^{-1} \qquad 7.1c$$

in which A_k is the relative space occupied by species S_k, Z_k the seed rate and b_k the crowding coefficient of species S_k; there being $(n - 1)$ independent crowding coefficients. The constant m is the surface of the unit square in figure 1.

It follows from 7.1 that

$$A_j = b_j Z_j \left[\sum_{k=1}^{n} b_k Z_k \right]^{-1} \qquad 7.2$$

so that, the yield being proportional with the relative space and M_j being the yield of species S_j when planted alone at a seed rate m^{-1}, the yield of species S_j in mixed culture is

$$O_j = b_j Z_j \left[\sum_{1}^{n} b_k Z_k \right]^{-1} M_j = b_j z_j \left[\sum_{1}^{n} b_k z_k \right]^{-1} M_j \qquad 7.3$$

in which z_j is the relative seed frequency i.e.

$$z_j = Z_j \left[\sum_{1}^{n} Z_k \right]^{-1}$$

The relative reproductive rate of species S_k with respect to species S_j is equal to

$$\alpha_{kj} = [O_k Z_k^{-1}]\,[O_j Z_j^{-1}]^{-1} = [b_k M_k]\,[b_j M_j]^{-1} \qquad 7.4$$

and thus again independent of the composition of the mixture.

Consequently, the values of the $(n-1)$ independent relative crowding coefficients $(b_k b_j^{-1})$ may be obtained by cultivating the species in $(n-1)$ combinations of two under the same conditions.

It is convenient to express the relative reproductive rates with respect to an arbitrary reference species S_i. The relative reproductive rate of this reference species is then equal to one, whereas the following equation for the relative reproductive rate of two arbitrary species S_k and S_j hold:

$$\alpha_{kj} = \alpha_{ki}\alpha_{ji}^{-1} \qquad 7.5$$

It will be shown in section 8.2. that these equations are strictly applicable, only, if the growth curves of single growing plants of the species are similar.

For a further analyses it suffices to consider three species S_1, S_2 and S_3 which are supposed to be grown in combinations of two at different relative seed frequencies, but otherwise under the same conditions.

7.2. A NUMERICAL EXAMPLE

Let it be supposed that a mixture of three species, S_1, S_2 and S_3 which affect each other only by crowding for the same space, is resown year after year at the same seed rate under exactly the same conditions and that the seed frequencies in the first year are $z_1 = 0.8$, $z_2 = 0.1$ and $z_3 = 0.1$ and that the relative reproductive rates are given by $\alpha_{3.2} = 1.8$ and $\alpha_{3.1} = 2.1$.

The ratio of the seed frequencies of S_3 and S_2 at the nth year may now be calculated with

$$[z_3\, z_2^{-1}]_n = 1.8^{n-1}$$

and of the seed frequencies of S_3 and S_1 with

$$[z_3\, z_1^{-1}]_n = 0.125 \times 2.1^{n-1}$$

equations which are obtained by substituting numerical values in equation 1.7.

The resulting relative frequencies of S_1 with respect to S_2 and to S_3, are plotted in the diagram of figure 30a along two sides of the tri-angle for a succession of ten years. The relative reproductive rate is not affected by the presence of a third species. Hence, the seed frequencies of the mixture of three species in for instance the third year may be represented by a point on the intersection of the line between the calculated value along the S_1–S_3 side for this year and the opposite corner and the line between the calculated value on the S_1–S_2 side for this year and the opposite corner. The relative frequency of S_3 with respect to S_2 may be found by drawing the third line. The calculated points for a period of ten years are given. In subsequent years

the relative frequency of S_1 and S_2 decreases still more until only the species S_3 is left.

The relative frequency of the species in the mixture of all three species is also represented in figure 30b, with the number of years along the horizontal axis. The winning species gains from the beginning and the loosing species looses from the beginning. The 'intermediate species', however, gains as long as the frequency of the loosing species is not negligible but looses from the sixth year onwards, when the relative frequency of the loosing species is small.

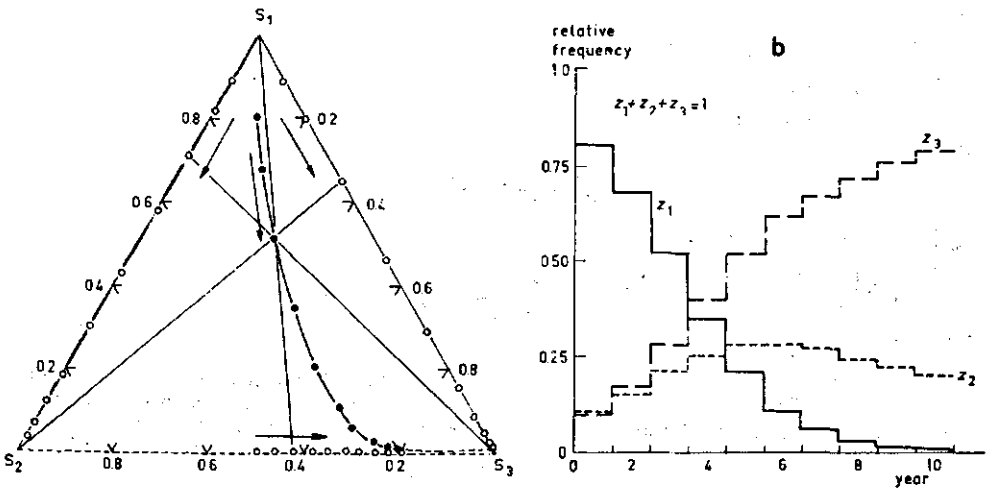


FIG. 30. A numerical example of the change in relative frequency during course of time at constant seed density, if three species affect each other only by crowding for the same space, α_{32} and α_{31} being 1.8 and 2.1, respectively.

HARLAN and MARTINI (1938) cultivated during a period of thirteen year a mixture of 10 barley varieties at different places in the United States. From each harvest 500 seeds were laid out, to obtain plants which could be determined as to variety. These investigators found indeed that a 'winning' species gains each year, a 'loosing' species looses each year and an 'intermediate' species gains first and looses subsequently. They showed that such a behaviour is to be expected if the reproductive rates are independent of the relative seed frequencies, but could not demonstrate the correctness of the underlying hypothesis because the growing conditions varied too much from year to year. This model used by HARLAN and MARTINI is the same as our simplest model discussed in section 1. It is shown in this paper that such a model does not conform with experimental results.

However, it is not necessary to assume that the reproductive rates are constant to illustrate this behaviour of a mixture. The assumption that the *relative* reproductive rates are independent of the seed frequencies is sufficient; an assumption which may do, because it is already shown that this is the case for barley–oats mixtures.

The actual relative frequencies of three out of ten species during 13 years as found in Aberdeen (table 2 of HARLAN and MARTINI) are given in figure 31. These three

species are chosen as an example, this sampling being allowed because the relative frequencies are probably not affected by the presence of other species. From an inspection of the actual data, it is estimated that the relative reproductive rate of the variety White Smyrna with respect to the variety Hannchen is about 1.06 and of White Smyrna with respect to Deficiens about 1.64. Starting from relative seed frequencies of 0.33 in the first year, the frequencies in subsequent years are calculated. These calculated values are given by the three lines.

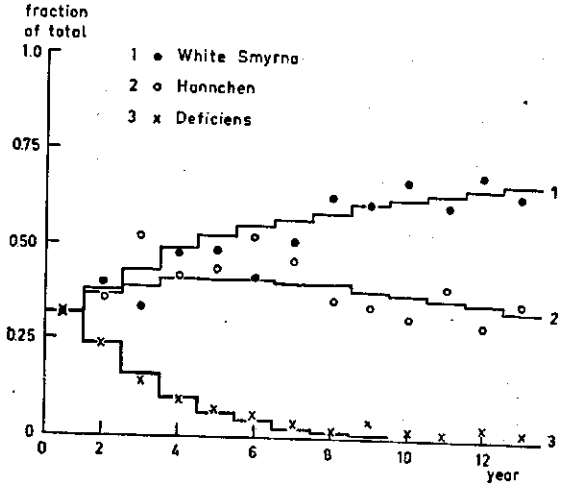


FIG. 31. The relative frequency of three barley varieties obtained by resowing during 13 years. Data for Aberdeen from HARLAN and MARTINI (1938).

The scattering of the points is considerable because of two reasons. In the first place, the relative reproductive rates vary from year to year because the growing conditions are not the same and in the second place, there must be considerable random sampling errors because only 500 seeds were analysed to determine the relative frequencies of 10 varieties. In spite of these fluctuations it is seen that indeed the 'intermediate' variety gains first and looses subsequently.

These data are only of illustrative value. The assumption that the three varieties affect each other only by crowding for the same space can neither be proved nor disproved by means of this type of experiment.

8. CROWDING FOR THE SAME SPACE WITHIN MIXTURES OF TWO OR MORE SPECIES AT DIFFERENT SPACINGS

8.0. SUMMARY

The basic equations, describing the interrelations between yield, seed rate, relative crowding coefficient and relative reproductive rate at different spacings are arrived at by supposing that one of the species in a mixture does not grow at all.

These basic equations are found to hold only if the plants grow simultaneously and the growth curves of the plants of the species are of the same form. It is shown that they are a particular solution of the LOTKA-VOLTERRA equations.

The equations are applied on the results of field experiments with mixtures of barley and oats and oats and peas, and on the well-known results of the experiment of GAUSE (1934) on population growth of protozoa under constant conditions.

8.1. THE BASIC EQUATIONS

The yield of the jth species is according to section 7.1 equal to

$$O_j = b_j Z_j \left[\sum_0^n b_k Z_k\right]^{-1} M_j \qquad 7.3$$

if $(n + 1)$ species are crowding for the same space, the space allotted to one seed being independent of the seed frequencies or $\sum_0^n Z_k$ being equal to m^{-1} (figure 1).

Let it be supposed now that the first species S_0 does not grow at all. Since there are only n independent crowding coefficients, it may be assumed that the crowding coefficient of this first not growing species is equal to one, so that the relative crowding coefficient of the remaining n species are equal to the crowding coefficients, i.e. that

$$k_{j0} = b_j \qquad 8.1$$

Equation 7.3 may be written now as follows:

$$O_j = b_j Z_j \left[\sum_1^n b_k Z_k + Z_0\right]^{-1} M_j \qquad 8.2$$

According the equations 5.2 and 8.1 the following relation holds:

$$b_j = [\beta_j + m]m^{-1} \qquad 8.3$$

The yield M_j of species S_j when planted at a spacing of m cm^2 per kernel is according to equation 5.4

$$M_j = \beta_j[\beta_j + m]^{-1}\Omega_j \qquad 8.4$$

Now the following relation is arrived at by substituting equation 8.3 and 8.4 in equation 8.2

$$O_j = \beta_j Z_j \left[\sum_1^n \beta_k Z_k + m \sum_0^n Z_k \right]^{-1} \Omega_j$$

As $\sum_0^n Z_k$ is equal to m^{-1}, this equation may be rewritten as follows

$$O_j = \beta_j Z_j \left[\sum_1^n \beta_k Z_k + 1 \right]^{-1} \Omega_j \qquad 8.5$$

β_k and Z_k being expressed in such units that their product is without dimension.

The relative reproductive rate of species S_k with respect to S_j is according to equation 8.5

$$\alpha_{kj} = [O_k Z_k^{-1}] [O_j Z_j^{-1}] = [\beta_k \Omega_k] [\beta_j \Omega_j]^{-1} \qquad 8.6$$

in which the product $\beta_j \Omega_j$ is the reproductive rate or yield of one seed of species S_j sown alone (eq. 5.5).

The relative crowding coefficient of species S_k with respect to species S_j is equal to (see equation 8.1)

$$k_{kj} = b_k b_j^{-1} = [\beta_k + m] [\beta_j + m]^{-1} \qquad 8.7$$

Equation 8.5 relates the yield of one arbitrary species in a mixture of n species with the absolute seed rates of the n species by means of the constants β and Ω for each species, constants which can be calculated from the results of spacing experiments.

Equation 8.6 shows that the relative reproductive rate of one species with respect to another is fully independent of the absolute seed rates of any of the species and therefore also independent of the density of sowing. To estimate the relative reproductive rates within a mixture of n species it is only necessary to determine the yield of one seed of each species when planted far apart from other seeds.

The relative crowding coefficient of one species with respect to another depends on the value of m. This relative crowding coefficient approaches at very wide spacings ($m \to \infty$) to unity; the plants do not affect each other under such conditions. The maximum value of the relative crowding coefficient is reached at very dense seed rates ($m \to 0$) and equal to the ratio of the values of β for both species.

8.2. The applicability of the formulae

It was already mentioned in section 3.2. that the crowding coefficients do not characterize the activity of crowding itself but only the result of this crowding as reflected in the final yields. This was experimentally demonstrated in section 5.2.1. by means of the result of a spacing experiment with sugar beets, harvested at intervals. It was found there, that the value of β increases more or less proportionally with the weight of the leaves during growth.

The formulae of the preceding section contain only constants calculated from the *final* harvests of the spacing experiments. If it is found for instance that the product $\beta\Omega$ for two plant species is the same, it is to be concluded according to equation 8.6 that the relative reproductive rate is 1 and independent of the seed rate. It is, however, perfectly possible that one of the crops is earlier in its development than the other. This is of course of small importance if both crops are sown together at a very wide spacing because under such conditions sufficient space is available for both. At a dense seed rate or at a small spacing, the available space may, however, already be occupied by the earlier species at the time the later species is in its grand period of growth. This advantage must result in a relative reproductive rate of the earlier species with respect to the later species which is greater than one, in spite of the fact that the product $\beta\Omega$ as calculated from the final yields is the same for both species.

This effect of spacing on the value of the relative reproductive rate is of course absent if the ratio $[\beta_k\Omega_k]\,[\beta_j\Omega_j]^{-1}$ (as calculated from dry weights obtained by periodic harvests of spacing experiments) does not depend on the time of harvest.

Hence the basic equation 8.5 can only be applied if the species affect each other only by crowding for the same space and the growth curves of single growing plants of the species are similar, that is the same apart from a multiplication factor of the yield axis. The relative reproductive rate is independent of the relative seed frequencies and of the absolute seed rates (or the value of m), only under these conditions.

On the other hand, the equations 3.4 can be applied provided that the experiments are carried out in such a way that the seed rate of the mixture is kept constant (i.e. such that equation 3.1a or b holds) and the two species affect each other only by crowding for the same space. That is because even with dissimilar growth curves, the ratio $[\beta_k\Omega_k]\,[\beta_j\Omega_j]^{-1}$ may be practically constant during the period the space is actually claimed. This period falls late in the growing period if m is large and early in the growing period if m is small. The relative reproductive rate is under such conditions found to be independent of the relative seed frequency, but depends on the seed rate of the mixture.

It is now evident that two species can only crowd for the same space if they grow simultaneously. The same space may be used first by the earlier species and subsequently again by the later species, if the species do not grow simultaneously, so that such species do not exclude each other completely. The relations which can be applied under such conditions are discussed in section 9.

It is emphasized again that 'space' is not defined in terms with a physiological meaning, so that any attempt to describe exactly the conditions under which the equations hold must fail.

8.3. The Lotka-Volterra equations on competition

The growth of a population of one species in a number of years was calculated in section 6.1. by substituting for the space per plant in the spacing formula the inverse of the yield of the previous year. It was proved in section 6.3. that in this way a solution of the differential equation for logistic growth is obtained.

Analogous relations are obtained by substituting the yield at the time t and $t+\Delta t$ (in which Δt is a fixed time interval) for the seed rates (Z) and the yields (O). For two species S_1 and S_2, this leads to the following equations:

$$O_1^{(t+\Delta t)} = \beta_1 O_1^{(t)} [\beta_1 O_1^{(t)} + \beta_2 O_2^{(t)} + 1]^{-1} \Omega_1$$
$$O_2^{(t+\Delta t)} = \beta_2 O_2^{(t)} [\beta_1 O_1^{(t)} + \beta_2 O_2^{(t)} + 1]^{-1} \Omega_2 \qquad 8.8$$

Thus if the seed rates are known in one year, the yields and seed rates in subsequent and preceding years may be calculated with these formulae, if the constants β and Ω are known from spacing experiments and provided that the growing conditions are the same.

VOLTERRA (1928) supposed that the growth of two populations living in the same environment may be governed by the following differential equations:

$$dO_1(dt)^{-1} = \{ r_1 - \gamma_1 [h_1 O_1 + h_2 O_2] \} O_1$$
$$dO_2(dt)^{-1} = \{ r_2 - \gamma_2 [h_1 O_1 + h_2 O_2] \} O_2 \qquad 8.9$$

By omitting the term $h_2 O_2$ in the first differential equation and after some rearrangement it is seen by comparison with equation 6.3 that r_1 is the coefficient of increase of species S_1 and $r_1[\gamma_1 h_1]^{-1}$ the maximum or equilibrium density of the species under the conditions of growth.

It is shown in textbooks on the subject that a partial solution of these differential equations is the following:

$$O_2^{\gamma_1} O_1^{-\gamma_2} = e^{(r_2\gamma_1 - r_1\gamma_2)t} \times \text{constant} \qquad 8.10$$

which after introducing the constant time interval Δt and eliminating the constant may be written as follows:

$$\{ O_2^{(t+\Delta t)} [O_2^{(t)}]^{-1} \}^{\gamma_1} \{ O_1^{(t+\Delta t)} [O_1^{(t)}]^{-1} \}^{-\gamma_2} = e^{(r_2\gamma_1 - r_1\gamma_2)\Delta t} \qquad 8.11$$

On the other hand it follows from equation 8.8 and 6.6 that

$$\{ O_2^{(t+\Delta t)} [O_2^{(t)}]^{-1} \} \{ O_1^{(t+\Delta t)} [O_1^{(t)}]^{-1} \}^{-1} = e^{(r_2 - r_1)\Delta t} \qquad 8.12$$

The equations 8.11 and 8.12 are the same if is supposed that VOLTERRA's constant γ_1 and γ_2 are both equal to one.

The basic equations 8.5 and 8.6 are therefore solutions of the following simplified LOTKA-VOLTERRA differential equations:

$$dO_j(dt)^{-1} = [r_j - \sum_1^n r_k K_k^{-1} O_k] O_j \text{ with}$$
$$\beta_j = [e^{r_j \Delta t} - 1] K_j^{-1} \; ; \; \Omega_j = e^{r_j \Delta t} [e^{r_j \Delta t} - 1]^{-1} K_j \qquad 8.13$$

The particular solutions 8.8, apart from the simplified form, are used by LESLIE (1958) and LESLIE and GOWER (1958) to study the influence of stochastic variations on population growth (compare section 6.4.).

8.4. CROWDING FOR THE SAME SPACE BY OATS AND BARLEY OR PEAS

8.4.1. *The design of the experiments*

In order to test the applicability of the basic equations in section 8.1. for field crops, experiments were carried out with oats (var. Libertas), barley (var. Herta) and peas (var. Pauli) on a field of the experimental farm 'Droevendaal' at Wageningen in 1959.

The normal spacing was supposed to be 31 cm^2 per seed for barley and oats and 139 cm^2 per seed for peas. One seed of peas is supposed to be equivalent with 4.5 seeds of oats or barley.

The occurrence of this factor 4.5 at inconvenient places in the equations is avoided by introducing the number of 'pea units', which is calculated by multiplying the number of peas in the sown mixture and in the harvest with the factor 4.5. Consequently for the seed rates of oats and pea units grown in competition holds equation 3.1a with m equal to 31 cm^2 per seed.

Experiment IBS 245 was carried out with oats and peas. The treatments were (1) mono culture of oats at a spacing of 310, 238, 169, 99, 31, 15.5, 7.7 and 3.8 cm^2 per kernel, (2) mono culture of 'pea units' at the same spacings and (3) mixed culture of oats and 'pea units' at relative frequencies of 0.111, 0.222, 0.333, 0.444, 0.555, 0.666, 0.777 and 0.888 on basis of a spacing of 31 cm^2 per kernel of oats or per pea unit.

Since it was the purpose to study the effect of the nitrogen fixed in the nodules of the peas on the growth of oats, no nitrogen was added. It appeared that this complicating effect was completely absent, because of the nitrogen level of the field being high. Complications which occur, if such an interaction is not absent, will be discussed in section 9.

Experiment IBS 246 was carried out with oats and barley. The treatments were (1) mono culture of oats at the same spacings as in experiment IBS 245, (2) mono culture of barley at the same spacings, (3) mixed culture of barley and oats at relative frequencies of 0.2, 0.4, 0.6 and 0.8 on basis of a spacing of 31 cm^2 per seed and (4) mixed culture of barley and oats at the same relative frequencies but on basis of a spacing of 310 cm^2 per seed.

Nitrogen was applied at a rate of 30 kg N per hectare.

Both experiments were laid out in a 5×5 lattice with two replicates, but a correction of the experimental data for differences of fertility level of the sub-plots was found to be not worth the trouble and any how not trusted.

8.4.2. *The treatment of the experimental results*

The results of the competition experiment between barley and oats at a spacing of 31 cm^2 per seed are given in figure 32a and those for a spacing of 310 cm^2 per seed

in figure 32b. The curves are calculated according to the equations 3.4, the numerical values of the constants being:

for m	equal to	31	and 310	cm^2 kernel^{-1}
M_b		123	85	10^6 kernels ha^{-1}
M_o		162	102	10^6 kernels ha^{-1}
k_{bo}		2.3	1.2	—
α_{bo}		1.75	1.02	—

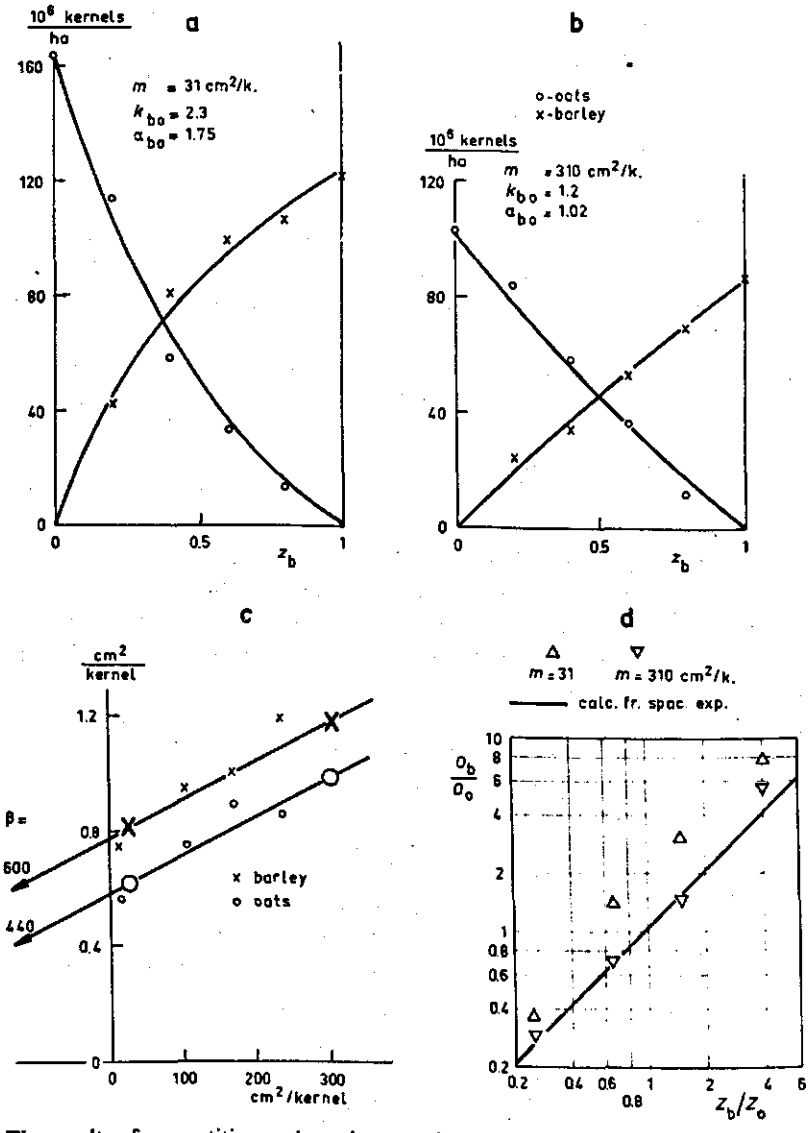


FIG. 32. The results of competition and spacing experiment IBS 246 between barley and oats in 1959.

The results of the spacing experiments with both crops are given in the graph of figure 32c with along the horizontal axis the spacing in cm^2 $kernel^{-1}$ and along the vertical axis the inverse of the yield in cm^2 $kernel^{-1}$.

The marks at a spacing of 31 and 310 cm^2 $kernel^{-1}$ represent the M_b and M_o values from the graphs of figure 32a and 32b. The statistical weight of these average data is much higher than the weight of the data for the other spacing. They are therefore represented by marks of a larger size. The average straight line through the points is mainly based on these two observations. The scattering of the other observations is considerable, but it will be seen that the estimated constants of the spacing formula (5.4) as given below are accurate enough for the purpose.

oats	barley	
$\beta_o = 440$	$\beta_b = 600$	cm^2 $kernel^{-1}$
$\Omega_o = 170$	$\Omega_b = 130$	10^6 kernels ha^{-1}

The observations for spacing of 7.7 and 3.8 cm^2 $kernel^{-1}$ are already discussed in section 5.1.3., and of no importance here.

The result of the competition experiment between oats an 'pea units' at a spacing of 31 cm^2 per kernel or 'pea unit' is represented in figure 33a, the curves being calculated according to the equations 3.4. The numerical values of the constants are: $m = 31$ cm^2 per kernel, $M_p = 102 \times 10^6$ pea units per ha, $M_o = 132 \times 10^6$ kernels of oats per ha, $k_{po} = 0.20$ and $\alpha_{po} = 0.16$.

The results of the spacing experiments with both crops are given in the graph of figure 33b with along the horizontal axis the spacing in cm^2 per kernel or cm^2 per pea unit and along the vertical axis the inverse of the yield in the same units.

The points at a spacing of 31 cm^2 per kernel represent the M_p and M_o values as read from the graph of figure 33a. These are again represented by marks of a larger size than the other observations, because the statistical weight is much higher than of the other observations.

The estimated constants of the spacing formula (5.4) are given in the following table:

oats	pea units	
$\beta_o = 580$	$\beta_p = 100$	cm^2 $kernel^{-1}$
$\Omega_o = 135$	$\Omega_p = 132$	10^6 kernels ha^{-1}

8.4.3. *Discussion of the experiment with oats and peas*

The relative crowding coefficient of the 'pea units' with respect to the oats at a spacing of 31 cm^2 per kernel as calculated from the spacing experiments by means of equation 8.7 is equal to $k_{po} = [100 + 31]\,[580 + 31]^{-1} = 0.21$, whereas k_{po} calculated from the competition experiment equals 0.20. The agreement between both values is excellent. Likewise, the relative reproductive rate of the pea units with respect to oats as calculated from the spacing experiments by means of equation 8.6 is equal to $\alpha_{po} = [100 \times 132]\,[580 \times 135]^{-1} = 0.17$, and α_{po} as calculated from the competition experiment is equal to 0.16. The agreement is of course again excellent.

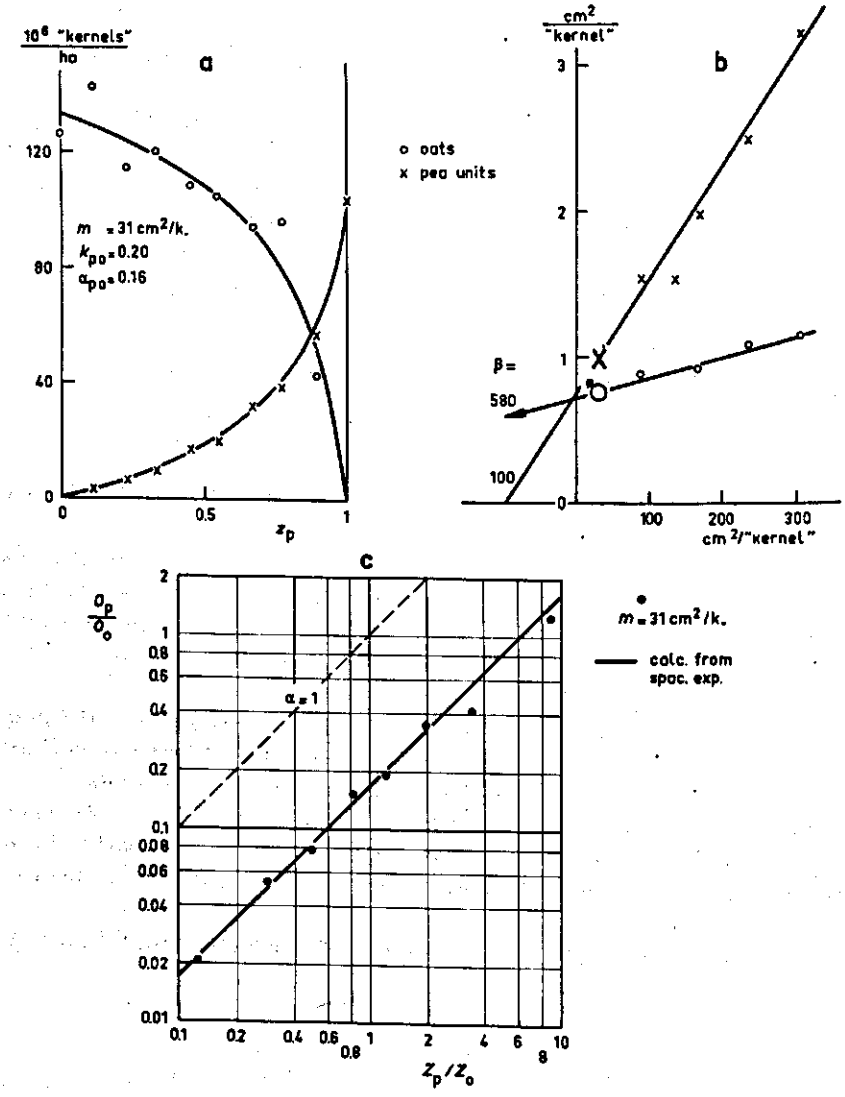


FIG. 33. The results of competition and spacing experiment IBS 245 between oats and peas in 1959. On pea kernel is equivalent with 4.5 'pea units'.

This agreement is also shown in the graph of figure 33c in which the relative reproductive rate for each mixture is represented by the dots and the relative reproductive rate as calculated from the results of the spacing experiments by the full drawn line. It must be concluded therefore that the result of competition experiments with oats and peas at any seed density can be calculated from the results of spacing experiments by means of the equations 8.5, under these conditions.

This conclusion does of course not mean that the growth curves of an oat and pea

plant are exactly similar, but only that the dissimilarity between the two curves is small compared with the difference of the values of $\beta\Omega$ for these two crops.

8.4.4. *Discussion of the experiment with oats and barley*

The relative reproductive rates of barley with respect to oats at the four relative seed frequencies and the two spacings of 31 and 310 cm^2 $kernel^{-1}$ are represented in figure 32d. It is seen that these relative reproductive rates are independent of the seed frequencies, so that it must be concluded (which was known of course) that the two plant species affect each other only by crowding for the same space.

However, the relative reproductive rate at a spacing of 31 cm^2 $kernel^{-1}$ is equal to 1.75, whereas this value at a spacing of 310 cm^2 $kernel^{-1}$ is only 1.02. Only this latter value is practically equal to the relative reproductive rate as calculated from the spacing experiments, which is 1.04 and is represented in figure 32d by the straight line.

The increase of the relative reproductive rate with decreasing spacing of the seeds proves according to section 8.2. that the growth curves of barley and oat plants are not similar, but that barley is earlier in its development than oats. This conclusion was confirmed by a competition and spacing experiment between rows of barley and oats on the same field in 1960, which was harvested at seven intervals throughout the growingperiod. It appeared that the products of $\beta\Omega$ in g dry matter per meter row of barley and oats were 80 and 30 on 15 May, 270 and 160 on 1 June, 510 and 430 on 15 June, and 680 and 640 on 1 July, respectively.

The difference appeared large enough to explain the effect of density on the relative reproductive rate. Unfortunately, the scattering of the yield data of the last harvest was so large that for a detailed analyses the experiment is to be repeated.

8.5. Crowding for the same space by protozoa

Gause (1934) described growth experiments with the protozoa *Paramecium caudatum* and *Paramecium aurelia* in his well-known book on the struggle for existence.

Accumulation of waste products and a gradual change of the liquid growth medium of 10 cm^3 was avoided by renewing the medium of growth every day. The supply of food was kept constant and at a low level by adding every day 'one half loop' of a standardized culture of *Bacillus pyocyaneus*. Every day the number of infusoria were counted in 0.5 cm^3 of the medium. Further details on this technique which were given by Gause are of small importance here.

The constants of the logistic growth curve (eq. 6.3), as calculated by Gause were for *P. aurelia* $r_a = 1.124$ day^{-1}, $K_a = 245$ individuals per 0.5 cm^3 and for *P. caudatum* $r_c = 0.794$ day^{-1}, $K_c = 64$ individuals per 0.5 cm^3, where r represented the coefficient of increase and K the maximum or equilibrium density which can be maintained.

The actual observations for growth in mono cultures and the curves calculated by Gause are given in figure 34a, in which for convenience the data for both species are recalculated at a basis of 100 units per culture for the equilibrium density.

The scattering of the observations is considerable. The coefficients of increase as calculated by GAUSE for the 'half loop' concentration are, however, confirmed by those for the 'one loop' concentration of bacteria. It is therefore in spite of this scattering evident that the coefficient of increase of *P. aurelia* is greater than of *P. caudatum*. The values of β and Ω for the two species for periods of two days can be calculated by substituting 0.794 day^{-1} and 1.124 day^{-1} in the equations 6.6 for the coefficient of increase of the two species and a density of 100 units per culture for the maximum or equilibrium density. The results are for *P. aurelia* $\beta_a = 0.085$ cultures per unit and $\Omega_a = 112$ units per culture and for *P. caudatum* $\beta_c = 0.039$ cultures per unit and $\Omega_c = 126$ units per culture.

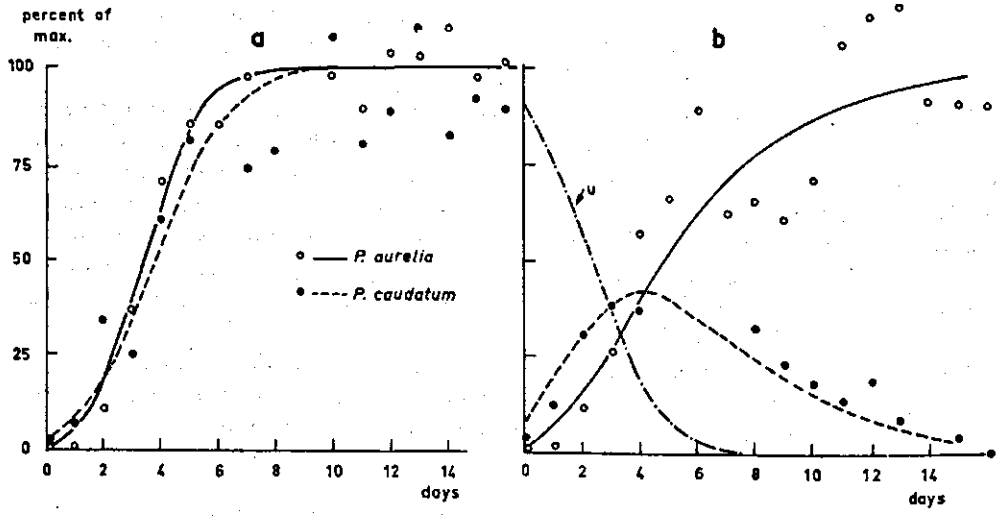


FIG. 34. The results of an experiment on intraspecific and interspecific population growth of two *Paramecium* species. Data from GAUSE (1934).

The yield of both species, cultivated in mixed culture at the time $(t + 2)$ days may be estimated by means of equation 8.5 by substituting for the seed rates the yields at the time t and for the constants β and Ω the numerical values given above.

This gives the following relations:

$$O_a^{(t+2)} = 0.085\, O_a^{(t)}\,[0.085\, O_a^{(t)} + 0.039\, O_c^{(t)} + 1]^{-1}\ 112 \quad \text{units per culture}$$

for the yield of *P. aurelia* and

$$O_c^{(t+2)} = 0.039\, O_c^{(t)}[0.085\, O_a^{(t)} + 0.039\, O_c^{(t)} + 1]^{-1}\ 126 \quad \text{units per culture}$$

for the yield of *P. caudatum*.

GAUSE started a mixed cultivation with two individuals per 0.5 cm^3 of each or with $O_a^{(o)}$ equal to $2 \times 100/245 = 0.816$ and $O_c^{(o)}$ equal to $2 \times 100/64 = 3.13$ units per culture. By substituting these values in the above equations, the yield after two

days may be calculated and by substituting again these yields, the yields after again 2 days and so on. The data obtained in this way may be compared with the resulting curves. However, large deviations may occur because especially during the first few days the actual data are subject to relatively very large random errors. This difficulty, due to random deviations can be avoided by substituting at some later date two values which match the actual data for the yield.

The numbers as observed by GAUSE in mixed cultivation of the two species are given in figure 34b. It is seen here that at the fifth day the yield of *P. aurelia* is about 52 and of *P. caudatum* about 40 units per culture. These values are substituted in the equations 8.5, to obtain the yields at the days $(5 + 2)$ and $(5 - 2)$, and these yields are again substituted to calculate the yields at the days $(5 + 4)$ and $(5 - 4)$, and so on. The resulting calculated growth curves for the two species are given in the graph of figure 34b.

As far as the observations go, the agreement between the observed growth curves and the growth curves calculated from the data of the mono cultures of the two species is reasonable.

Since at any time there are infusoria in different stages of development in the culture vessel it is not, however, allowed to conclude from this that the growth curves of the individuals of both species are similar.

The sum of both curves represents the relative space which is actually occupied by both species, since the yields of both species separately are recalculated at a basis of 100 for the equilibrium or maximum density. The difference of this sum and 100 is therefore the unoccupied space or the space occupied by an imaginary not growing species. This unoccupied space is represented by a third curve (u) in order to show the similarity with the graph of figure 30b.

The relative reproductive rate of *P. aurelia* with respect to *P. caudatum* for periods of Δt days is according to the equations 8.6 and 6.8 equal to

$$\alpha_{ac} = [\beta_a \Omega_a]\,[\beta_c \Omega_c]^{-1} = e^{(r_a - r_c)\Delta t}$$

or in this case 1.94 for periods of two days. Apparently the species with the largest coefficient of increase is the winning species.

This conclusion was also arrived at by BIRCH (1953) who cultivated three beetle species (*Rhizopertha dominica* and the small and large strain of *Calandra oryzae*) alone and in combinations of two under conditions of constant food supply. On the other hand, FRANK (1957), who cultivated *Daphnia magna* and *Daphnia pulicaria* as mono cultures and in combination, found that this was not the case and that the two species may promote the growth of each other.

The result of this experiment of FRANK (1957) is only mentioned to stress that there are closely related species which may effect the growth of each other also by other means than only crowding for the same space. Under such conditions the relations as given here do not hold of course.

9. AN ANALYSIS OF MORE COMPLICATED WAYS OF COMPETITION

9.0. SUMMARY

Plant species may affect the growth of each other in other ways than simply crowding for the same space. The relative reproductive rate depends in all these cases on the relative seed frequency. A stable equilibrium may result if the species crowd for space which is only partly the same for both or if one of the species promotes in some way the growth of the other. An unstable equilibrium occurs, however, only if one of the species hampers the growth of the other not only by crowding for space, but also by some active process like producing intoxicants.

Some examples are given in the next section.

9.1. THE USE OF THE RELATIVE REPRODUCTIVE RATE AND THE RATIO DIAGRAM

One of the simplest forms of competition occurs if two plant species affect each other only by crowding for the same space (which implies that the species grow simultaneously) and the growth curves of single plants of both species are similar. The relative reproductive rate is independent of the relative seed frequency and the spacing under such conditions.

The observations in a ratio diagram are in this case on a straight line with a slope of 45 degrees, of which the position is independent of the spacing. This situation is schematically represented in figure 35a, where the seed ratio $Z_1Z_2^{-1}$ is given along the horizontal axis and the yield ratio $O_1O_2^{-1}$ along the vertical axis, both with a logarithmic scale. This ratio diagram was discussed in section 1.1.4. Species one wins in this case because the ratio line is above the equilibrium line $\alpha = 1$. The direction in which the composition of the mixture changes during cultivation is represented by the arrow. Either one species or the other wins at any spacing.

The relative reproductive rate is only at a given spacing practically independent of the relative seed frequency if two species affect each other by crowding for the same space, but the growth curves for single plants are not similar. Under such conditions, situations as represented in the ratio diagram of figure 35b may occur.

Here it is supposed that species one is earlier in its development but otherwise inferior to species two. This earlier development is of no use at wide spacings, so that species one looses. At narrow spacings, this earlier development is of very great importance, so that species one wins. Which species is winning depends therefore on the spacing.

The spacing decreases rapidly if the harvest is resown year after year, so that ultimately species one is always winning. An equilibrium between both species is only possible if the spacing is kept at such a value that the relative reproductive rate is one. Hence to decide which of two species wins, it is necessary to determine the relative

reproductive rate at or near the maximum or equilibrium density, which is reached if all available space is occupied.

The competitive relations are still more complex if there is crowding for space, not completely the same for both species. This may occur if some requisite obtained from the soil (water, minerals) is limiting growth and species two explores the soil

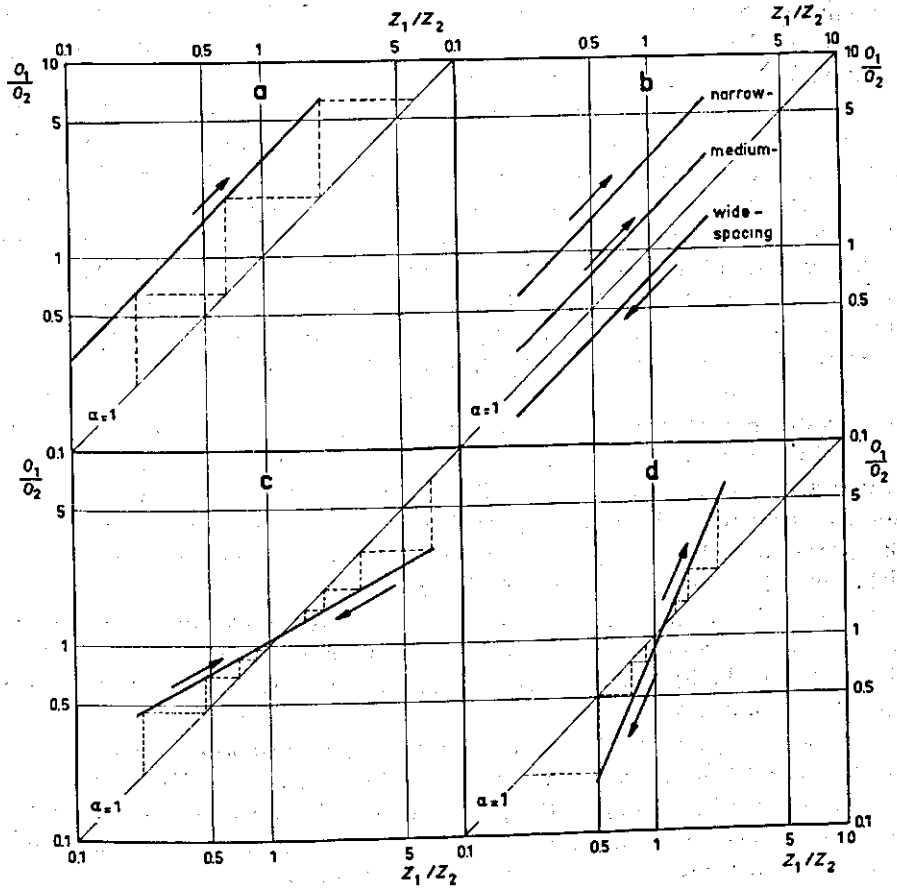


FIG. 35. Schematical representation of ratio diagrams for two species,
a. which crowd for the same space and with similar growth curves,
b. which crowd for the same space and with not similar growth curves,
c. of which the presence of one promotes the growth of the other, or which crowd for space not being completely the same for both species,
d. of which the presence of one hampers the growth of the other by other means than simple crowding for space.

to a greater depth than species one. It occurs also if species two grows longer or at another period of the year than species one, so that species two may occupy space which was at some earlier period occupied by species one. Species two must grow under such conditions better according as the relative frequency of this species is

lower. Hence the relative reproductive rate of species two with respect to species one decreases with increasing relative frequency of species two, so that a situation as represented in figure 35c may result. The ratio line intersects here the equilibrium line $\alpha = 1$. Species two wins in this case if its relative frequency is low, and looses if its relative frequency is high, so that ultimately a stable equilibrium of both species may result, which value is given by the ratio at the point of intersection of both lines. It is shown in the next section that the curve is not straight but S-shaped with the ends parallel to the diagonal if the total seed rate of the mixture is kept constant.

It is of much importance that a stable equilibrium may result also if one of the species profits from the presence of the other. This may occur if one of the species obtains nitrogen from the air *(legumeneous species)*, one of the species liberates minerals from the soil which can be used by the other, and so on.

The relative reproductive rate as calculated from the experiment with peas and oats, discussed in section 8.4.3., is independent of the relative seed frequency. The absence of any effect on oats due to nitrogen fixation by peas is shown in this way.

The reverse of this case, presented in figure 35d, occurs if one of the species hampers the growth of the other not only by crowding for space, but also by some active process as producing an intoxicant which hampers the growth of the other species.

The relative reproductive rate of species one with respect to species two must increase with increasing relative frequency of species one under such conditions. The ratio line may intersect again the equilibrium line $\alpha = 1$. The equilibrium obtained is, however, unstable under such conditions. Species one wins if the relative frequency of this species is higher and species two wins if the relative frequency of this species is higher than the relative frequency at the point of intersection.

It has been shown that some plants or seeds produce intoxicants with a selective effect on other species (GRÜMMER, 1955). There is, however, considerable doubt as to the question whether the production is so large that some effect remains under normal field conditions.

GRÜMMER (1955) carried out some experiments with *Linum usitatissimum* (flax) and the weed *Camelina foetida* and came to the conclusion that *Camelina* produces some unknown matter which hampers the growth of *Linum*. However, the interpretation of the experiments is difficult because the data do not permit the calculation of the relative reproductive rates at the same spacing of the mixtures.

To investigate a possible toxic effect, an experiment was carried out in the green house, in which *Linum usitatissimum* (flax) and *Camelina sativa* (false flax) were cultivated in pots at three different relative frequencies (exclusive of the mono cultures), but at the same spacing. The result as calculated on basis of the kernel numbers is represented in figure 36. The relative reproductive rate seems to depend to some extent on the relative seed frequency. This is probably due to experimental errors, which are unavoidable in a first experiment with new plant species. There is, however, no indication that the relative reproductive rate of *Linum* with respect to *Camelina* increases with increasing relative frequency of the *Linum*. Hence any effect of intoxicants, large enough to be shown in this way, was absent under the conditions of this experiment.

Later on GRÜMMER (1958) came to the conclusion that this adverse effect of false flax on flax occurs only if the mixtures are subjected to rain. This effect of rain was not confirmed by an experiment on competition between *C. sativa* and flax under conditions of artificial rain and of sub-irrigation (DE WIT, 1960). However, it was found by GRÜMMER (pers.com., 1960) that *C. sativa* produces much less toxic substances than *C. foetida*.

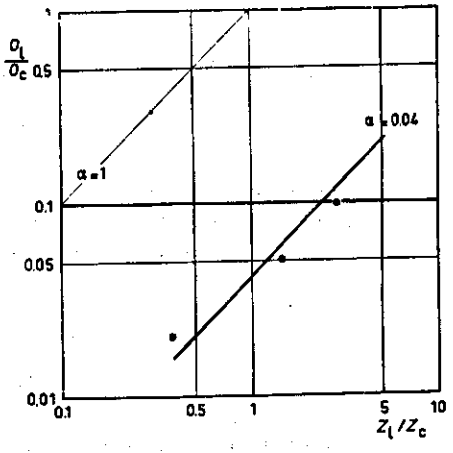


FIG. 36. The ratio diagram as calculated from a green house experiment on competition between flax (O_1, Z_1) and false flax (O_r, Z_r).

9.2. CROWDING FOR PARTLY THE SAME SPACE WITHIN MIXTURES OF TWO SPECIES

The yield of two species sown in such a way that the seed rate of the mixture satisfies the equation

$$Z_1 + Z_2 = m^{-1} \qquad 3.1a$$

is considered.

According to section 3.2., the yields satisfy the following equations if the two species affect each other only by crowding for the same space:

$$O_1 = k_{12} z_1 \{[k_{12} - 1]z_1 + 1\}^{-1} M_1 \qquad 3.4b$$

$$O_2 = k_{21} z_2 \{[k_{21} - 1]z_2 + 1\}^{-1} M_2$$

with $z_1 = Z_1[Z_1 + Z_2]^{-1}$ etc. The product of the constants k_{12} and k_{21} is equal to one in these equations.

The yield of the species, in case both crowd for space which is completely different, is of course given by the spacing formula developed in section 5., which may be written in the following form

$$O_1 = k_{1e} z_1 \{[k_{1e} - 1]z_1 + 1\}^{-1} M_1 \qquad 5.1$$

$$O_2 = k_{2e} z_2 \{[k_{2e} - 1]z_2 + 1\}^{-1} M_2$$

in which the constants

$$k_{1e} = [\beta_1 + m]m^{-1} \text{ and } k_{2e} = [\beta_2 + m]m^{-1} \qquad 5.2b$$

are the relative crowding coefficients of the species with respect to their own 'empty spaces'.

Both sets of equations are the same, apart from the product of the relative crowding coefficients.

This product is equal to

$$k_{12} \cdot k_{21} = 1 \qquad 9.1$$

if the two species crowd for the same space and equal to

$$k_{1e} \cdot k_{2e} = [\beta_1 + m]\,[\beta_2 + m] m^{-2} \qquad 9.2$$

if the species crowd for space which is completely different for both.

The most plausible supposition which can be made is now that in case two species crowd for space which is partly the same, the yields may be represented by the following set of equations.

$$\begin{aligned} O_1 &= k_{1(2e)} z_1 \{[k_{1(2e)} - 1] z_1 + 1\}^{-1} M_1 \\ O_2 &= k_{2(1e)} z_2 \{[k_{2(1e)} - 1] z_2 + 1\}^{-1} M_2 \end{aligned} \qquad 9.3$$

The indices of the relative crowding coefficients mean that one species is supposed to crowd for space with the other species and 'empty space'. The product of these relative crowding coefficients is somewhere between the minimum value of equation 9.1 and the maximum of equation 9.2.

The relative reproductive rate of species S_1 with respect to species S_2 is according to equation 9.3 equal to

$$\begin{aligned} \alpha_{12} &= [O_1 Z_1^{-1}]\,[O_2 Z_2^{-1}]^{-1} = \\ &= \{k_{2(1e)} - 1] z_2 + 1\}\,\{[k_{1(2e)} - 1] z_1 + 1\}^{-1}\,[k_{1(2e)} M_1]\,[k_{2(1e)} M_2]^{-1} \end{aligned} \qquad 9.4$$

Apparently, the value of α_{12} increases with decreasing z_1, Z_1, $z_1 z_2^{-1}$ or $Z_1 Z_2^{-1}$, the limits being $k_{1(2e)} M_1 M_2^{-1}$ for $Z_1 Z_2^{-1}$ approaching 0 and $k_{2(1e)}^{-1} M_1 M_2^{-1}$ for $Z_1 Z_2^{-1}$ approaching ∞.

The value of α_{12} in equation 9.4 and the values of β_1 and β_2 in the equation 5.2b are to be multiplied by $c_1 c_2^{-1}$, c_1^{-1} and c_2^{-1} if the seed rates satisfy the equation

$$c_1 Z_1 + c_2 Z_2 = m^{-1}. \qquad 3.1b$$

in stead of equation 3.1a (compare section 3.2.).

A numerical example is given in figure 37. The yield curves in figure a are calculated by means of the equations 9.3, supposing $M_1 = M_2 = 100$ and $k_{1(2e)} = k_{2(1e)} = 3$. The sum of both yields $(O_1 + O_2)$ shows in this case a maximum of 150 at a relative frequency of 0.5, which illustrates that mixed cultivation of crops may be advantageous if the species crowd for space which is not completely the same. The ratio curve, which is S-shaped is given in figure b. The maximum and the minimum relative reproductive

rate appear to be 3 and 1/3, respectively. The curve intersects the diagonal at $Z_1 Z_2^{-1}$ equal to one. It is obvious that the ratio curve is not symmetrical if $M_1 \neq M_2$ or (and) $k_{1(2e)} \neq k_{2(1e)}$ and that the whole curve may be found above or below the diagonal if the growth of the two species differs widely. It can also be shown that the maximum of $(O_1 + O_2)$, if any, does in general not coincide with the equilibrium point, if any. This is the Montgomery effect (section 3.4.) in this complicated situation.

Formally, the equations 9.3 can only be applied if it is known that two species affect each other only by crowding for space, which is not completely the same. Since

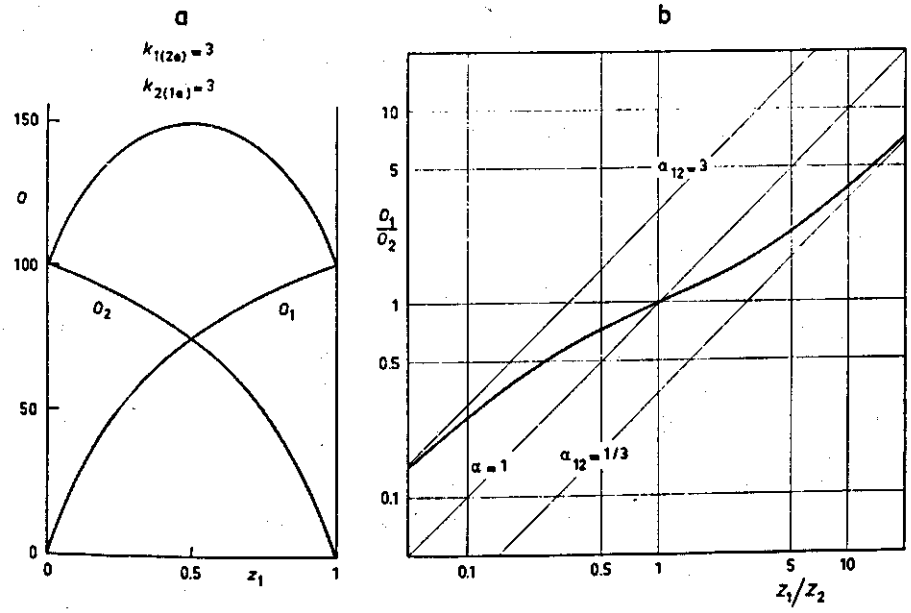


FIG. 37. a. An example of the relation between the relative seed frequency and the yield of two species S_1 and S_2, crowding for space which is only partly the same.
b. The ratio diagram with an S-shaped ratio curve.

it is difficult to determine the physiological causes of nonconstancy of the relative reproductive rate, the same equations may be used also in first instance if the species affect the growth of each other in some other way.

The most convenient approach is to treat the data by means of the equations 9.3 and to calculate subsequently the product of the relative crowding coefficients. The species crowd for the same space if this product is one. They crowd for space which is partly the same or one species profits from the presence of the other if the product is larger than one. One species hampers the growth of the other by some other mains than crowding for space, if the product is smaller than one. It remains to be seen, however, whether in this case the data can be conveniently smoothed by the equations 9.3.

10. COMPETITION BETWEEN PERENNIAL GRASSLAND SPECIES

10.0. Summary

It is shown that the competitive relations between perennial grassland species can be analysed by counting the number of tillers of each species per surface unit in two subsequent winters or dormant periods.

Some results of experiments with *Anthoxanthum odoratum* and *Phleum pratense* and with *Lolium perenne* and *Trifolium repens* are given as an example.

10.1. The relative reproductive rate of perennial grassland species

It was shown in the preceding sections that the form of the curve in the ratio diagram or the dependence of the relative reproductive rate on the relative frequency gives valuable information on the competitive relations between two species.

The relative reproductive rate of two seed producing annual species can be calculated from the composition of a sample of the seed mixture in two subsequent winters. Likewise, the relative reproductive rate of two perennial species can be calculated from observations during the rest period or winter. The yields during the growing period do not give any information in principle, because the harvested parts are lost as far as the plants are concerned.

De Wit and Ennik (1958) paid some attention to the problem of finding a good measure for the 'abundance of grassland species' in winter. The weight of the plant is not such a measure because it depends to a large extent on the arbitrary treatment in autumn and the presence of dead or partly dead material. Another disadvantage is that the weight can only be determined after destroying the plants.

Instead, it was suggested to use the number of tillers of the grass species and the length of stolons of clover per surface unit as a measure for the abundance of the species.

Ennik (1960) and van den Bergh and de Wit (1960) carried out some preliminary experiments to study the usefulness of this approach. The main results of their experiments will be discussed here.

10.2. Crowding for space between *Anthoxanthum odoratum* and *Phleum pratense*

Van den Bergh and de Wit (1960) planted these two species in different proportions in containers and studied their growth in climate chambers. The number of tillers of *A. odoratum* (Z_a) and *P. pratense* (Z_p) were counted after a summer treatment of some months followed by a winter treatment (6° C, 3×10^4 ergs cm^{-2} sec^{-1} from

TL-tubes during 12 hours a day) of one month. Subsequently a summer treatment (20^0 C, 6×10^4 ergs cm^{-2} sec^{-1} from HPL-lamps during 17 hours a day) of two months followed by the winter treatment of one month was given. The number of tillers of *A. odoratum* (O_a) and *P. pratense* (O_p) were again determined.

It appeared that the number of tillers of the two species at the end of the first winter treatment satisfied the following equation $Z_a + 1.75\,Z_p = 350$ 'tillers' per container so that the relative seed frequencies z_a and z_p can be calculated according to equation 3.5b.

The relation between the ratio's $O_a O_p^{-1}$ and $Z_a Z_p^{-1}$ is given in figure 38b. It appears that the observations are on a straight line with a slope of 45 degrees, so that the species affect each other only by crowding for the same space and the data can be treated by means of equation 3.4b.

The result is given in figure 38a, where the relative frequency z_a is given along the horizontal axis and the number of tillers (O_a and O_p) along the vertical axis. The curves in the figure satisfy the equations 3.4b with $M_a = 490$, $M_p = 290$ tillers per

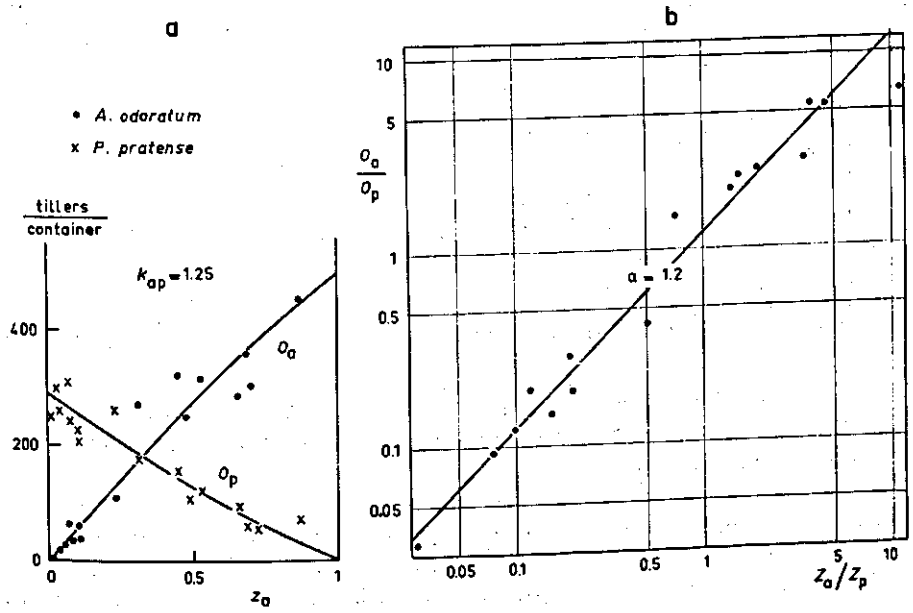


FIG. 38. The result of a competition experiment at constant spacing between the grass species *Anthoxanthum odoratum* and *Phleum pratense* in a climate chamber. Data from VAN DEN BERGH and DE WIT (1960).

container and $k_{ap} = 1.25$, so that the relative reproductive rate of *A. odoratum* with respect to *P. pratense* (α_{ap}) is according equation 3.7b equal to 1.2, which is represented by the full drawn line in figure 38b.

The same species were also grown in some kind of containers in the open. The number of tillers after the first and the second winter were again counted. The numbers

after the first winter satisfied the equation $Z_a + 1.53\ Z_p = 420$ 'tillers' per container so that again the relative frequencies z_a and z_p can be calculated.

The observations in the ratio diagram of figure 39b are now on some line with a slope smaller than 45 degrees, so that the yield data are to be treated by means of the equations 9.3 instead of 3.4b. The yield curves of figure 39a satisfy now these equations

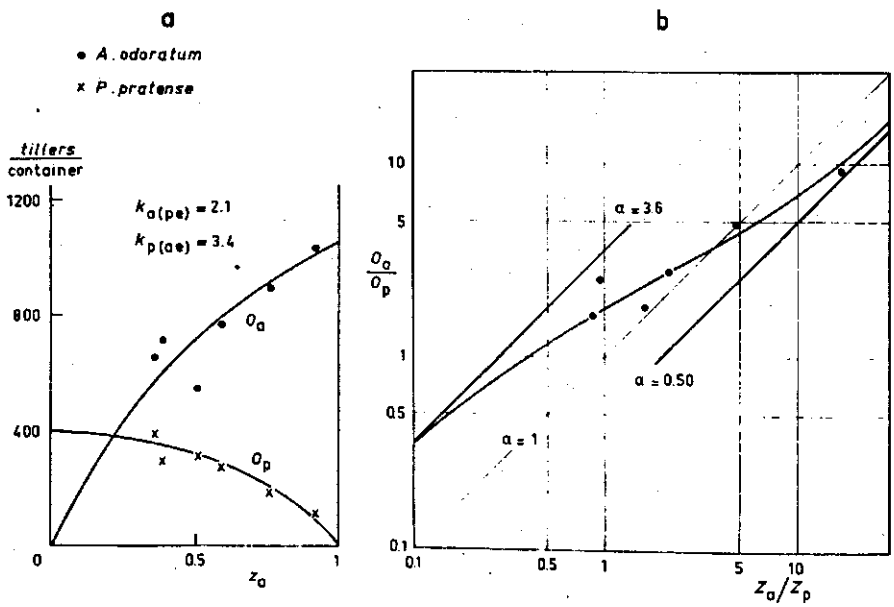


FIG. 39. The result of a competition experiment at constant spacing between the grass species *Anthoxanthum odoratum* and *Phleum pratense* in the field. Data from VAN DEN BERGH and DE WIT (1960).

9.3 with $M_a = 1050$, $M_p = 400$ tillers per container and $k_{a(pe)} = 2.1$ and $k_{p(ae)} = 3.4$ so that the product of the two relative crowding coefficients is 7.1, which is indeed appreciable larger than one.

The two species, grown in the open, crowd therefore either for space which is only partly the same or one species profits in some way from the presence of the other. This latter possibility can safely be excluded because no sign of it was found in the climate chambers. Moreover, the growth of the roots of the plants was in the open in a similar way restricted by the containers as in the climate chambers. The only reason why the space of the plants in the open is only partly the same is therefore that the growth and development of the species during the summer differ considerably from each other. Now it is indeed known that *A. odoratum* develops early in the summer season and the particular strain of *P. pratense* relatively late. This difference did not manifest itself in the climate chambers because here a 'summer treatment' without any seasonal trend in temperature, day length or light intensity was given.

The relative reproductive rate as calculated from the curves in figure 38a is represented by the full drawn curve in figure 38b. The equilibrium point appears to be at a

ratio of $Z_a Z_p^{-1}$ equal to 4 and the maximum and minimum reproductive rates are 3.6 and 0.50.

10.3. Competition between *Lolium perenne* and *Trifolium repens*

Ennik (1960) planted *Lolium perenne* and *Trifolium repens* in different proportions in containers and applied winter treatments and a summer treatment in the climate chambers which were essentially the same as those for the mixture of the grass species of the preceding section. The abundance of clover at the end of the winter treatments was characterized by the length of the stolons, and of *Lolium perenne* by the number of tillers per container.

The relative reproductive rates at different proportions are given in figure 40. The observations are again on some line with a slope smaller than 45 degrees, so that the data were treated by means of equation 9.3. Details on this treatment may be found

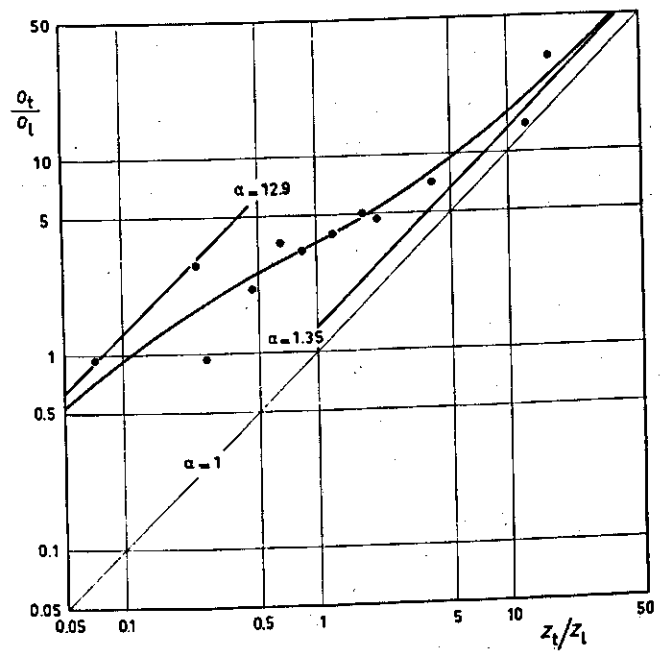


Fig. 40. The result of a competition experiment at constant spacing between the grassland species *Lolium perenne* (O_1, Z_1) and *Trifolium repens* (O_t, Z_t). Data from Ennik (1960).

in the original paper. The resulting curve in the ratio diagram is, however, represented also in figure 40. The maximum and the minimum relative reproductive rate appear to be 12.9 and 1.35, so that an equilibrium is not reached.

Clover and grass affect each other apparently in some other way than crowding for the same space. Ennik showed that in this particular case the clover obtained all its nitrogen from the air and the grass from the soil. Hence, the grass did not

profit from the presence of the clover, but the 'nitrogen spaces' were different for both species.

The competitive relations between *T. repens* and *L. perenne* at different water levels in the soil were also analysed by ENNIK (1960). The values of the relative crowding coefficients of the grass with respect to the clover and empty space ($k_{l(te)}$), of the clover with respect to the grass and empty space ($k_{t(le)}$), their product and the maximum and minimum value of the relative reproductive rates of the clover with respect to the grass are given in the following table:

waterlevel in cm below soil surface	$k_{t(le)}$	$k_{l(te)}$	$k_{t(le)} \times k_{l(te)}$	α_{tl} $z_t \to 1$	α_{tl} $z_l \to 1$
12	2.08	1.22	2.54	2.49	6.34
26	2.13	1.05	2.24	2.05	4.59
41	1.00	1.40	1.40	1.58	2.21
70	0.80	1.70	1.36	1.06	1.45
99	0.64	1.81	1.16	1.09	1.26

Details on the treatment of the experimental results and conclusions may be found in the original paper. Here it is only remarked that the two species crowded for nearly the same space at low water levels, but that the 'nitrogen spaces' appeared to be again practically different at high water levels.

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